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Electromyographic Patterns of Hand Muscles During Rhythmic Finger Movements and Handwriting

By

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A thesis submitted to the University of Bristol
for the degree of Doctor of Philosophy in the Faculty of Science

March, 1997

Department of Physiology
University of Bristol
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To my parents

ABSTRACT

Electromyographic patterns of hand muscles during repetitive finger movements and handwriting

Most recent physiological studies on hand muscles focused upon selected aspects of muscle performance under static conditions, often involving steady contractions, or functionally isolated reflex responses, rather than the co-ordinated, rhythmic activity of combinations of muscles required in such tasks as handwriting and repetitive finger movements.

Three main objectives have been addressed:

- (1) to identify characteristic co-ordination patterns of different hand muscles during rhythmic manipulatory tasks;
- (2) to compare hand muscle activity patterns produced by the standard dynamic tripod grip (DTG) and unusual pen-grips, e.g. four finger grasp (4FG) and five finger grasp (5FG) during component writing;
- (3) to assess the role of proprioceptive feedback by examining phase- and task-dependent reflex responses evoked by mechanical or electrical stimulation applied at various phases of repetitive finger movements akin to handwriting.

Surface electromyograms were recorded from six hand/forearm muscles in fifty four healthy subjects and two writer's cramp subjects during the movements. These included three hand muscles: flexor pollicis brevis, abductor pollicis brevis, 1st dorsal interosseous, and three forearm muscles: flexor digitorum superficialis, extensor digitorum communis, extensor pollicis brevis.

Motor co-ordination patterns were observed in antagonistic, synergistic muscles during rhythmic manipulations. All normal subjects showed stronger phasic modulation patterns of muscle activity in relatively isolated finger movements than in delicate, skilled tasks like handwriting. It is concluded that the sensory feedback may be more active in the latter tasks than the former ones.

Comparisons of muscle activity patterns show characteristic differences between the DTG, 4FG, and 5FG grips, suggesting an influence of posture in forming handwriting activity patterns.

Stretch reflexes were strongly modulated with respect to both phase and task in normal subjects during rhythmic finger manipulations. The results imply that this modulation pattern may reflect optimal motor strategies of central-peripheral interactions in controlling performance of skilled hand motor tasks.

SUMMARY

1. Electromyographic (EMG) activity has been simultaneously recorded from four of six intrinsic and extrinsic hand muscles involving the control of finger movements in fifty four normal subjects and two writer's cramp subjects during repetitive manipulatory tasks related to handwriting.
2. Hand muscle activity showed characteristic co-ordination patterns of antagonistic, synergistic muscles while performing a range of rhythmic manual tasks. 1st dorsal interosseous (1DI) showed comparable activity patterns to the thumb flexor during the tasks being carried out. The results suggest that 1DI plays a distinctive synergistic role in a variety of finger movements involving the metacarpophalangeal joint of the thumb.
3. EMG amplitude was modulated to a higher degree in relatively simple finger tasks than in highly skilled writing tasks, suggesting that sensory information and proprioceptive feedback might be more active in regulating the delicate, precise tasks than those relatively simple finger manipulations.
4. Muscle activity patterns of various postures of holding a pen, including the standard 'dynamic tripod grip', 'four finger grasp', and the uncommon 'five finger grasp' pen-grips, have been examined during the performance of discrete component writing tasks. The results showed comparable muscle activity patterns between the "dynamic tripod grip" and the "four finger grasp" pen-grips, but divergent patterns from the "five finger grasp". This implies that the posture of finger and thumb has a defined influence on handwriting motor output pattern.
5. Electromyographic reflex responses elicited in intrinsic and extrinsic hand muscles by mechanical stretch were highly modulated in gain as a function of the phase of the movement cycle. As implied also by comparable studies on locomotion, this may be

interpreted as indicating a dynamically fluctuating role of proprioceptive feedback, from sensory receptors in muscles and joints, in the movement control of the muscles performing the tasks.

6. Reflex responses to mechanical perturbation of the index finger during the three finger manipulatory tasks studied here were found to vary distinctly with the tasks being carried out. This task-dependent pattern is consistent with an interplay of sensory feedback and central programming, presumably adapted in characteristic ways to the particular motor performing task.
7. Writer's cramp subjects showed co-activation between antagonistic muscles during handwriting, but normal alternate activation during isolated finger movements. Stretch reflexes were modestly modulated in relation to phase and task in writer's cramp, in contrast to normal subjects, during rhythmic finger actions. These observations suggest that a defective interaction of central-peripheral systems may result in the abnormality of muscle performance during skilled hand movements.

ACKNOWLEDGEMENTS

I am particularly indebted to Dr. Brian Bush for his supervision, encouragement and many helpful discussions during these three years. Without his support, it would not have been possible. I also owe to Dr. Patricia Dolan for her patience, helpful discussions of the work through this period.

I would like to thank all the subjects who voluntarily participated in the experiments. Some of the subjects attended more than one experiment.

Thanks are also due to Mr. Tony Macdonald who designed and built some of the electronic apparatus for this project.

I would like to express my gratitude to the CVCP for awarding me an Overseas Research Scholarship (ORS) and the University of Bristol, Faculty of Science for a Postgraduate Research Scholarship.

DECLARATION

None of the work embodied in this thesis has been presented for any degree or diploma at any other University. Some of the results presented in Chapter 3 and 4 include data collected in collaboration with four 3rd-year BSc Physiology students. All the work and conclusions drawn in this dissertation are entirely based upon the independent work of the author.

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CHAPTER 1

GENERAL INTRODUCTION

Studies of motor control have occupied important positions in physiology, psychology and clinical neurology for over a century. The term ‘motor control’ refers to the study of movements and postures as well as to the functions of mind and body that govern movement and posture. Posture, in this context, means the static position of any part of the body, as this word suggests. Movement is the transition from one posture to another. The dictum of Sherrington (1906, 1915) -- “*Posture follows movement like a shadow; every movement begins in posture and ends in posture*” is applicable to the control of the body and limbs. Movements and postures can be assumed consciously or as automatic adjustments, a distinction that formerly denoted “voluntary” as opposed to “reflex” actions. Only rudimentary motor abilities come with birth, and the majority of motor behaviours are developed by learning later. For example, we have to learn to stand, to walk, to write, and to play various forms of sports. This learning is never directed at the control of a single muscle. A muscle is never used in an isolated way under normal circumstances. Even the simplest movements are performed via functional combinations of many different muscles that act on the joints at which they are inserted. Most movements depend on proprioceptive information from the peripheral sense organs, such as muscle spindles, joint receptors and cutaneous receptors, which are relayed to the spinal cord and brain. Sensory guidance used for either agonist or antagonist commands forms the closed-loop, feedback mode of control system. Programmed commands are remembered or stored and compared with the information arriving from sense organs in the periphery. Thus, the codes for intended movements can be examined by the performance output. Any detected errors between the intended and actual events can be corrected by intended as well as by automatic adjustments (Kelso, 1982; Brooks, 1986; Humphrey & Freund, 1991). Therefore, motor learning is concerned with the co-ordination of joints and muscles that move and hold these joints under both spatial and temporal environments, which requires the control of interaction between the central and peripheral nervous systems.

The main target for the neurophysiologists is to understand the complexity of the central nervous system (CNS) and how movements and postures are controlled by

central commands and spinal reflexes. A study of the sensory receptors, neural connections and effectors of basic reflex arcs provided valuable information for attempting to understand the central mechanism. Broad studies on anatomical and functional aspects of the reflex arc and of the integrative action of the *CNS* were first made by Sir Charles Sherrington. The principles governing these reflex arcs were subsequently established by Sherrington and summarised in his monograph (Sherrington, 1906). Since then, the knowledge and understanding of the reflexes were enormously expanded from his studies. Studies focused on spinal reflexes have been extensively reported for almost a century.

In recent years, investigations have concentrated on identifying which part of the brain is responsible for controlling movements and postures. Although there is much about the control of voluntary movement that is still unknown, there is considerable evidence in monkeys and humans for the general control scheme shown in Figure 1.1.

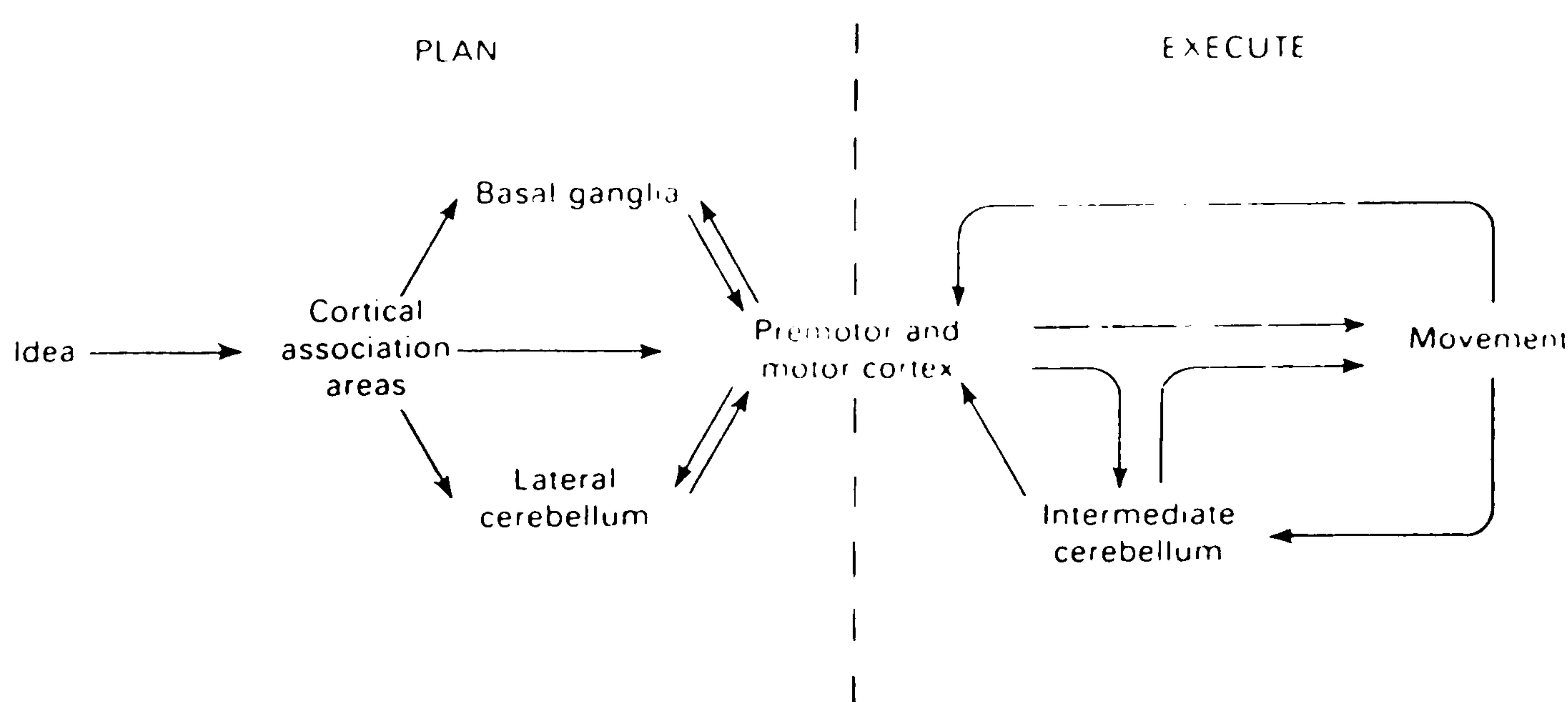


Figure 1.1. Control of voluntary movement (Modified from McGeer, P.L. & McGeer, E.G. (1980). The control of movement by the brain. *Trends in Neurosciences* 3, 3-4.)

Commands for voluntary movement originate in cortical association areas. The movements are planned in the cortex as well as in the basal ganglia and the lateral portions of the cerebellar hemispheres, both of which funnel information to the premotor and motor cortex by way of the thalamus. Motor commands from the motor cortex are relayed in large part via the corticospinal tracts and the corresponding corticobulbar tracts to motor neurones in the brain stem. However, collaterals from these pathways and a few direct connections from the motor cortex end on brain stem nuclei, which also project to motor neurones in the brain stem and spinal cord, and these pathways can also mediate voluntary movement. Movement sets up alterations in sensory inputs from muscles, tendons, joints and the skin. This feedback information which adjusts and smooths movement, is relayed directly to the motor cortex and to the spinocerebellum. The spinocerebellum projects, in turn, into the brain stem. The main brain stem pathways that are concerned with posture and co-ordination are the rubrospinal, reticulospinal, tectospinal and vestibulospinal tracts and corresponding projections to motor neurones in the brain stem (Ganong, 1991).

Motor control is studied at multiple levels, such as the movement level, the network or circuit level, and the cellular, synaptic or molecular level. Each level has its focuses on each different aspect. In this study, motor control of the human hand is studied at the movement level which involves the nervous system as well as the muscular system of the hand, i.e., electromyographic study.

Historical perspective of electromyography (EMG)

Electromyography (*electro* = electricity; *myo* = muscle; *graph* = to write) is defined as the evaluation of electrical activity in resting and contracting muscles. The record of the study is known as an electromyogram or EMG (Tortora & Anagnostakos, 1990).

The first logical deduction of muscle-generated electricity was documented by an Italian, Francesco Redi, in 1666. He suspected that the shock of the electric ray fish

was muscular in origin. The relationship between electricity and muscle contraction was first observed by Luigi Galvani in 1791. In his epoch-making experiments, he depolarised the muscles of a frog's leg by touching them with metal rods. His concept of animal electricity was enthusiastically received throughout Europe. This discovery is generally acknowledged as representing the birth of neurophysiology, thereby making Galvani the father of this field, which continues to develop rapidly. In 1820, Schweigger built the first practical galvanometer based on Oersted's discoveries on magnetism. Five years later, Nobili improved the sensitivity by compensating for the torque of the earth's magnetic field. Using this improved galvanometer, Carlo Matteucci in 1838 finally proved that electrical currents did originate in muscles. In 1844, he wrote:

“The interior of a muscle place in connection with any part whatsoever of the same muscle... produces a current which goes in the animal from the muscular part to that which is not so.”

Matteucci's work attracted the interest of the Frenchman DuBois-Reymond, who first reported the detection of voluntarily elicited electrical signals from human muscles in 1849. He devised a surface electrode which consisted of a wire attached to a blotting paper immersed in a jar of saline solution. Upon contraction, he measured a sizeable deflection on his galvanometer. However, measurements from human musculature remained unwieldy until the metal surface electrode was employed by the German Piper (1907). The advent of the cathode ray tube invented by Braun (1897) further simplified the detection technique which was first used to amplify action potentials in conjunction with a string galvanometer by Forbes and Thacher (1920). Two years later, Gasser and Erlanger (1922) used a cathode ray oscilloscope in place of the galvanometer to show the signals from the muscles. This application, along with their wise interpretation of the action potentials, earned Gasser and Erlanger a Nobel Prize in 1944.

During the 19th century, the capability of detecting the electromyographic or myoelectric signal from a human muscle remained a sophisticated and delicate venture.

In the middle of the 19th century, the French scientist Duchenne skilfully applied electrical stimulation to investigate systematically the dynamics and functions of intact skeletal muscles. His work has contributed much to our understanding of muscular function. Duchenne's book, *Physiologie des Mouvements*, has been translated into English by Kaplan in 1959.

The first known electrical model of the nervous system was made by the Englishman Baines, who published his work in 1918. He formalised the analogy between the propagation of pulses in a nerve trunk and an electrical cable. This approach subsequently became known as the cable theory. He initiated the concept of modelling parts of the nervous system with electrical circuits in attempting to explain their behaviours.

The task of detecting the electromyographic signal was greatly simplified by the introduction of vacuum tube amplifiers. Soon, the new approach of EMG was put to practical usage in the clinical environment. The first successful attempt at detecting a signal from a dysfunctional muscle was made by Proebster in 1928 who obtained "tracings" from a muscle with peripheral nerve paralysis. However, the impact on the clinical community occurred after the introduction of the needle electrode by Adrian and Bronk in 1929. This enabled us to observe the electrical activity associated with individual muscle fibres for the first time. In the 1950s and 1960s, the use of the needle electrode was methodologically exploited by Buchthal and his colleagues. With the improvement of quality and availability of electronics apparatus, electromyography has been paid much attention and has been increasingly used by anatomists, kinesiologists and orthopaedic surgeons etc. in diverse areas.

The foregoing section has introduced the electrical activity associated with a muscle contraction contributed by a wide variety of individuals during the past two centuries (summarised from "*Muscles Alive: Their Functions Revealed by Electromyography*" by Basmajian and De Luca, 1985).

Voluntary rhythmic activity and reflex function during locomotion

Locomotion means the act of moving from one position to another position, and includes various forms, e.g. walking, running, stepping, jumping, swimming, flying and so on. Locomotion is characteristically a rhythmic pattern, generated by a “central pattern generator” (*CPG*) in the spinal cord which, in turn, is activated and controlled by the brain stem and influenced by peripheral feedback mechanisms (Grillner, 1975, 1979), as first proposed by Brown in his “half centre” hypothesis (1911, 1914) and subsequently reintroduced by Lundberg (1969). *CPG* networks play a major role in modulating and interacting dynamically with proprioceptive feedback from joints and muscles (Grillner, 1985). The *CPGs* have also been assumed for other motor behaviours, such as breathing, chewing and hopping.

Locomotion, as a subject of interest, has been extensively studied in different species for some hundreds of years. In the 18th century, the investigation of movement was grounded on the perception that upright stance and gait, in association with the differentiation of hand movements, represented a basic requirement for humans. During all the motor activities performed in a bipedal posture, the nervous system automatically balances the body’s centre of mass over the feet. The methodical analysis of human gait began at the end of the 19th century, with the development of photographic recordings (“chronophotography”) of running and jumping movements by Marey (Marey, 1873, 1894). Using biomechanical recordings, Bernstein later (1936) resumed gait analysis. Electrophysiological recordings during locomotion were first performed in cats by Engberg and Lundberg (1969) and Grillner (1972). These studies were extended to record leg muscle electromyograms and the activity of muscle primary afferents in freely moving cats. Locomotion has been found to be based on three main components within the *CNS*: (1) a basic level generating rhythmical activity, central pattern generator; (2) supra-ordering structure controlling this elementary level; and (3) the sensory information (proprioceptive, cutaneous and articular) which interacts with the *CPG* (Grillner, 1981). The basic element of locomotion is the step cycle, which is composed of two phases: swing phase and stance phase. Schematically, the swing phase

corresponds to a flexion of most joints and stance to an extension of the locomotor appendages. In locomotion, many different muscles are involved, each of which is activated in a particular phase of the movement cycle. Switches from one phase to another phase are crucial points where proprioceptive and cutaneous cues may act as specific sensors. The co-ordination of these muscles is produced by the neural *CPG* networks modulating and interacting dynamically with sensory feedback from muscles and joints. The feedback is crucial for adaptation of the movement synergy to what happens during the movement. On the other hand, sensory signals activated by movements are of major importance in the sensory control. In recent years, an increasing number of locomotory studies have employed human subjects (Dietz, 1992; Stein, 1995).

The significance of the reflexes on central rhythms and programming in locomotion was present from the beginning of these investigations and their study continued in both animal and human studies. The best known example of a spinal reflex is the tendon jerk. It was first brought to the attention of scientists simultaneously in 1875 by Erb and Westphal, separately. Initially, the stretch reflex was regarded as the direct response of a muscle to percussion. Liddell and Sherrington (1924) recorded the stretch reflex in the quadriceps muscle in the decerebrate cat. It was demonstrated that the quadriceps jerk in the cat could be abolished by dorsal root section and thus the reflex nature of the response was confirmed. Hoffmann (1918) emphasised that in humans the tendon reflex mechanism is responsible for the adaptation of the muscle innervation to unexpected strains. Foerster (1921) suggested that slow stretch reflexes and “adaptonal reflexes” made an essential contribution to motor co-ordination. Several models, such as the length servo hypothesis by Merton (1953), and the stiffness regulation hypothesis of Houk (1979) have been proposed and tested against experimental data since the discovery of the stretch reflex.

A reflex analogous to that of the tendon jerk may also be evoked in some muscles by stimulating the nerve trunk electrically. Electrical stimulation of the

posterior tibial nerve in the popliteal fossa evokes a contraction of the calf muscles. This was first shown by Piper in 1912 and then clearly described by Hoffmann (1918, 1922), who demonstrated that the response observed consisted of a short latency and a delayed activation of the motor units of the triceps surae muscle. The reflex had a latency of about 30 ms and was believed to be the electrical analogue of the tendon jerk (T-reflex). The reflex-elicited contraction of the calf muscles was due to activation of group Ia afferent fibres from spindle primaries and became known as the Hoffmann reflex or H-reflex in his honour.

During the performance of all motor acts, the movements of the animal or human need to be continuously adapted to match the changing environmental conditions. Reflexes are highly modulated by the central nervous system during functional motor tasks and the modulation appears to be task-dependent (Lennard & Hermanson, 1985; Capaday & Stein, 1986, 1987; Stein & Capaday, 1988; Edamura, Yang & Stein, 1991; Dietz, 1992; Stein, 1995). Reflexes may play a role in adapting the movement to changing demands from the environment in order to achieve the desired movement trace, in both animals and humans (Dietz, Schmidtbleicher & Noth, 1979; Grillner, 1979). It has been demonstrated that reflexes elicited by cutaneous stimuli are modified depending on the phase of the step cycle during walking in cats (Forssberg, Grillner & Rossignol, 1975, 1977; Duysens & Stein, 1978). Studies in humans have also shown that spinal reflexes can be modulated to adapt motor programs to actual requirements. For example, the H-reflex is strongly modulated in a number of muscles as a function of time during cyclical movements (Garrett, Ireland & Luckwill, 1984; Capaday & Stein, 1986, 1987; Dietz, Faist & Pierrot-Deseilligny, 1990; Edamura, Yang & Stein, 1991; Brooke *et al.* 1995). Similar results have been obtained in the investigation of the spinal stretch reflex which assists triceps surae contraction during the stance phase of running (Dietz, Schmidtbleicher & Noth, 1979; Dietz & Noth, 1983). These observations suggest that, in both animals and humans, spinal reflexes play a role in adapting the movement to changing demands from the environment in order to achieve the desired movement trajectory.

From a functional point of view, it is difficult to compare the motor control in upper and lower limbs due to the functionally different demands of the two systems in general motor performance. The upper limb normally functions predominantly under voluntary control. In considering the central and reflex mechanisms available for automatic motor control, the programmed muscle activation in the upper limb takes place in a similar fashion to that seen in the leg muscles with respect to both the structure of the pattern and the mode of pre-activation. Moreover, the behaviour of group I-mediated segmental reflexes appears similar in upper and lower limbs. However, transmission and function of the long-latency or polysynaptic reflexes seem to differ (Dietz, 1992).

Motor control of movements of the hand

A normally functioning hand is of great importance in earning a living, manipulating tools or leading independence in daily activities. As described in the book “*The Physiology of the Joints*” by Kapandji (1987):

“The human hand, despite its complexity, turns out to be a perfectly logical structure fully adapted to its multiple functions. Its architecture reflects Occam’s principle of universal economy. It is one of the most beautiful achievements of nature”

Skilled hand movements are essential for our culture. Without these, there would be no art, no communication, no science and technology. The human hand is capable of the strongest grasp and the most delicate touch. In Old World monkeys, apes and man, Napier (1956) has differentiated power and precision grips: power, in use of the whole hand for supporting weight or wielding heavy objects; precision, in picking up small objects with thumb and index finger, whose sensitive tips can be brought into pulp-to-pulp contact by the elemental movements of flexion and opposition. Using combinations and sequences of the elemental movements of flexion, extension, abduction, adduction and opposition of thumb and index finger, man’s highest

manipulative skills, like drawing, painting, writing, watch-making, microelectronics, microsurgery, are built up (Phillips, 1986).

One of the major issues in hand motor control is how the central nervous system governs and regulates voluntary movement of the hand, and which part of the brain is involved in the control of the hand movement. The primary motor cortex (M1) of the cerebral cortex is the essential part of the brain involved in the control of the distal muscles of the extremities. Figure 1.2 illustrates the general view of a monkey's cerebral cortex including primary motor cortex (Brodmann's area 4) which plays an important role in controlling normal voluntary movements. Figure 1.2, AB is obtained from a parasagittal slice through the arm areas related to the hand.

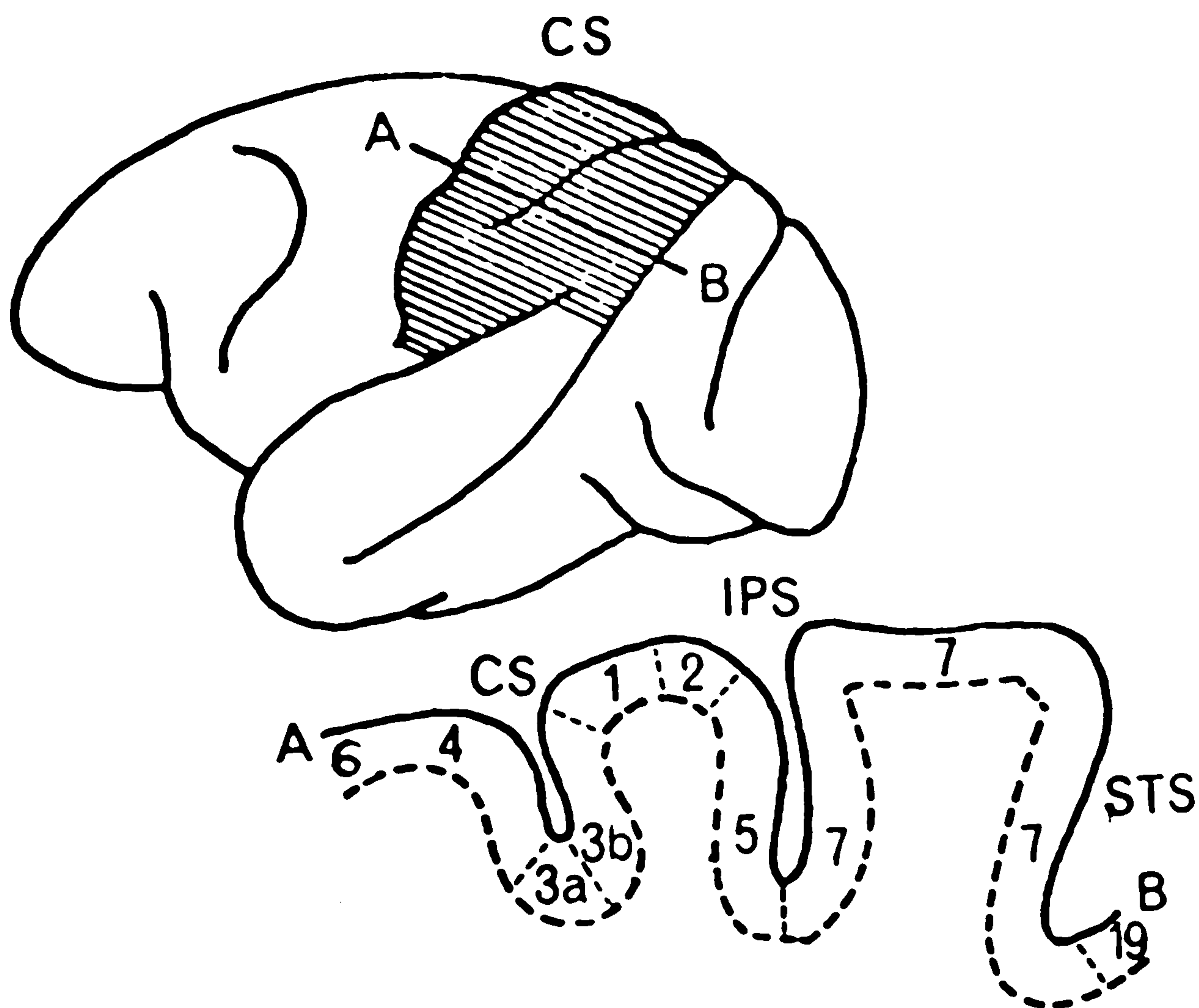


Figure 1.2. Cortical areas related to the hand. The location of the parasagittal slice AB is marked on the outline of the left hemisphere of a monkey's brain. Numerals are Brodmann's. Areas 3a, 3b, 1 and 2 together constitute the primary somaesthetic receiving area. CS: central sulcus; IPS: intraparietal sulcus; STS: superior temporal sulcus. (Gordon, *Active Touch*, 1978. Pergamon Press, Oxford)

The areas are basically similar in men and monkeys, but are much larger in man. The motor cortex was first identified in electrical stimulation experiments. The lowest threshold points for a motor response are found to lie in the motor cortex while applying an electrical stimulus to the cerebral cortex. Such stimuli evoke discrete movements of distal muscles on the contralateral side. When the hand representation is stimulated, the contralateral hand moves. The areas with the lowest threshold for electrical stimulation are Brodmann's areas 4, 6 and 8. Electrical stimulation of area 4 finds a large hand area in monkeys and men. Many of the experiments on the subdivisions of the frontal cortical areas have been performed on monkeys. Brodmann's areas 4 and 6 contain the main motor areas of the frontal cortex. Experimental work has indicated the special contribution of M1 to the independent finger actions (Travis, 1955; Hamuy, 1956; Lawrence & Kuypers, 1968). The labelled-line hypothesis predicts that movements of different fingers are controlled from spatially separate parts of M1. The motor cortex has a topographic organisation which is demonstrated by summary drawings made in the monkey by Woolsey (Woolsey *et al.* 1951) and in man by the neurosurgeon Penfield (Penfield & Rasmussen, 1950). These drawings show a motor map of the contralateral body parts laid out on the M1 cortex. The hand is represented more laterally on the convexity of the cerebrum. The anatomical studies have shown that the caudal part of the motor cortex is in a position to influence directly the activity of motoneurons to the hand and digit muscles.

Apart from M1, other cortical areas can also evoke movements when stimulated with more intense stimuli. Motor areas of the cerebral cortex also include the premotor area which helps control proximal and axial muscles, the supplementary motor cortex which participates in motor planning and in co-ordination. The premotor cortex receives a major input from the posterior parietal cortex, and its output influences mainly the medial system of descending pathways. These connections suggest that this region of cortex controls the axial muscles. Neurons in this area seem to discharge during preparation for a movement. The supplementary motor cortex is involved in motor planning and is active during both the planning and the execution of complex

movements. Its actions are partly mediated by direct corticospinal connections, but they partly depend on a relay to the primary motor cortex. Besides its role in motor planning, the supplementary motor cortex may assist in the co-ordination of posture and voluntary movements. Rhythmic movements can sometimes be elicited from this area of cortex.

The classical view of voluntary control of dexterous hand movements which emphasised the final common path function of the motor cortex requires revision. Recent studies suggest that the homuncular analogy is inappropriate for the neural control of the hand. A genuine understanding of the relation between brain and hand must take account of the hierarchical organisation of several different representations of the hand muscles, projecting in a many-to-many fashion onto the numerous muscles of the human hand. A clear example of how the marionette analogy of hand movement control has been replaced by the concept of a distributed, many-to-many mapping between cells in the motor cortex and the muscles of the hand has been provided by Schieber (1996). Schieber shows that the movement of an individual finger is not produced by activity in a labelled line in the motor cortex. Instead, moving a single finger requires contracting several muscles, many of which function as fixators to prevent the major muscle contraction from moving additional fingers. A similar multiple representation applies in the primary motor cortex: recordings from cells in monkeys trained to carry out single finger movements showed that many cells are active when the monkey moves any one of a number of digits. This result implies that a given cortical area represents more than one digit. Experimental evidence suggests that cortico-motoneuronal (CM) projections, mainly derived from the caudal part of the primary motor cortex, play a unique role in the execution of skilled hand movements. This projection is made up of corticospinal fibres having direct, monosynaptic connections with spinal motoneurons, and particularly with those motoneurons innervating hand and finger muscles. Comparative studies performed on different species of adult primates indicated that CM cells are probably essential for the ability to perform relatively independent finger movements (Armand, 1982; Lemon, 1983).

Voluntary movement and function of the human hand

Even in the simplest hand movements, there is a potential activation of a multiplicity of muscles. The major task for the motor control system is not only to contract the agonist, or prime moving muscles at the proper time and by the correct amount, but also to time and organise the pattern of antagonist, fixator and postural muscle contractions which are necessary to accompany its action. The variable spatial and temporal activation of many muscles and joints represent the optimal conditions for performing hand tasks and movements. The possible experimental strategy is to examine individual, discrete finger movements in the intrinsic or extrinsic hand muscles as most recent physiological studies have focused on. Using wire electrodes recording electromyography in all the muscles moving the middle finger, a series of excellent experiments performed by Long and Brown (1964) and their colleagues have greatly helped us in understanding of the function and activity of intrinsic and extrinsic muscles and their kinesiology, although the functions of the muscles and tendons that drive the fingers have been discussed for many years (Duchenne, 1867; Bunnell, 1948; Landsmeer, 1963). Increasing attention has been paid to the movement of fingers within the last several decades. Most of these studies have centred on specific aspects of muscle performance either in essentially static conditions or independent movement of a particular digit (Lawrence & De Luca, 1983; Darling & Cole, 1990; Bremner, Baker & Stephens, 1991).

Another important function of the hand is to grasp objects with different kinds of shape. The complex structure of the hand and wrist is indicated by its comprising 27 bones and 39 muscles located either in the forearm or in the hand that move the wrist and digits. The number of muscles exceeds the number of degrees of freedom provided by the joints. Due to its high number of degrees of freedom, the hand can perform highly complex movements. Our hand is able to grasp a broad range of objects with different shapes and sizes in our daily life. To reduce the complexity, prehensile activities of the hand can be classified into two types by looking at the function of the hand as a whole. Napier (1956) concluded that there exist only two types of prehension movements.

“The object may be held in a clamp formed by the partly flexed fingers and the palm, counter pressure being applied by the thumb lying more or less in the plane of the palm. This is referred to as the power grip. The object may be pinched between the flexor aspects of the fingers and the opposing thumb. This is called the precision grip.”

This stresses the general idea of a reduction of degrees of freedom, among the many possible ones, despite a small number of classifications. Tip-to-tip pinch grip, which is often used in fine manipulations, shows that there are at least 15 muscles contributing directly or indirectly to the production of force. Besides the long finger and thumb flexors, the intrinsics and wrist and finger extensors are of great importance in providing stability during the grip. One of the first detailed descriptions of the muscle functions of thumb, index and middle finger during pinch grip was given by Close and Kidd (1969). They recorded finger motion and EMG activity simultaneously from six to eight muscles. It was observed that there was co-activation of many muscles. This muscle synergy was confirmed by Long *et al.* (1970).

Role of proprioception in the control of hand movement

It has been well known that the proprioceptive system processes the information arising both centrally and peripherally about movement and the relative position of the body (Matthews, 1988). This information is used to control the movement and to correct for unexpected external disturbances from the environment in order to achieve the desired movement trajectory during the performance of functional movements. In the execution of delicately adjusted movements which require an optimal motor performance, the sensory information becomes particularly important. It is assumed that normal proprioceptive feedback is a prerequisite for motor tasks. Furthermore, it may be hypothesised that the ability to perform highly skilled manual tasks is associated with superior proprioceptive capabilities (Jones, 1996). A number of recent publications on a deafferented human subject have provided evidence that the ability to perform fine

manipulative tasks is impaired in the absence of proprioceptive information (Rothwell *et al.* 1982; Marsden, Rothwell & Day, 1984; Ghez *et al.* 1990; Teasdale *et al.* 1993).

One approach to evaluate the role of proprioceptive feedback in the control and execution of movements is to test spinal reflexes. Basic spinal reflexes have been extensively studied for over a century. Most of these investigations were performed under steady state conditions. A variety of stimuli, mechanical, electrical or cutaneous, can be applied to evoke reflex responses in voluntarily activated muscles. Intrinsic hand and extrinsic forearm muscles have been employed to investigate these reflex mechanisms (Darton *et al.* 1985; Evans, Harrison & Stephens, 1989; Matthews, 1989, 1993; Noth *et al.* 1991; Doemges & Rack, 1992a, 1992b). The classical descriptions of the stretch reflexes over at least the period 1945-70 attributed it entirely to the activity of the Ia afferents, on the basis of work on the cat. However, other pathways, including Ib fibres from the Golgi tendon organs, and the group II fibres from the spindle secondary endings, are suspected to be contributing to the response (Matthews, 1970). For humans, it has come to be generally accepted that the stretch reflex comprises two separate components: the classical short-latency reflex referred to as M1, followed by a long-latency component (M2) of more complex origin (Marsden, Merton & Morton, 1976). It is generally believed that the short-latency reflex response is mediated by fast conducting group-Ia fibres via a monosynaptic pathway. Investigations performed on the long-latency reflex component or M2 response have attracted many neurophysiologists within the last 25 years or so. The origin of the long-latency EMG response evoked from a human muscle is still under debate (Matthews, 1989, 1993). Generally, it is accepted that primary muscle spindle afferents (Ia fibres) contribute to the long-latency response to muscle stretches. This view is supported by a few studies on distal muscles in the upper limb (Darton *et al.* 1985; Noth *et al.* 1991). They suggested that it is the central processing in the spinal cord that delays the M2 response. Recent studies suggested that different mechanisms may be involved in the generation of the long-latency stretch reflex elicited in human hand and forearm muscles. Observations obtained in patients with neurological disorders indicated that M2 components in distal hand muscles are

probably relayed via the motor cortex and the corticospinal tract (Noth, Podoll & Friedemann, 1985; Matthews, Farmer & Ingram, 1990). Further evidence suggested that other mechanisms also contribute to the generation of the delayed components (Matthews, 1991; Thilmann *et al.* 1991).

The H-reflex has been recognised for nearly a century. Those that have been reported are mostly evoked in leg muscles of the lower limb during locomotion (Capaday & Stein, 1987; Edamura, Yang & Stein, 1991; Brooke *et al.* 1995). However, H-reflexes studied on human hand muscles are relatively few (Nakashima *et al.* 1990; Burke *et al.* 1992a, 1992b). In these studies, H-reflex responses were elicited by electrically stimulating the median nerve or radial nerve to record EMG responses from finger flexors in the forearm.

The foundation of our knowledge of cutaneous reflexes in mammals was established by Sherrington (1910), who made an extensive study of the hind limb in the decerebrate cat. Sherrington showed that electrical stimulation of a peripheral nerve resulted in flexion of the stimulated limb and extension of the contralateral one. Subsequently, Hagbarth (1952) found, by stimulating areas of skin rather than nerve trunks, that the distribution of excitatory and inhibitory effects was more subtle and purposeful than had been supposed. Cutaneous reflexes are usually seen as variations in the activity level in the tonically contracting hand and forearm muscles (Caccia *et al.* 1973; Evans, Harrison & Stephens, 1989). Responses are elicited by electrically stimulating the digital nerve of the fingers while producing a constant contraction of one or more muscles. A cutaneous reflex has generally been shown to comprise three main phases: a short latency excitation (E1) followed by an inhibition (I1) and a later excitation (E2). The E1 and I1 components are believed to be mediated by spinal reflex pathways, whereas the E2 component is considered to be of supraspinal origin requiring the integrity of the dorsal columns, sensorimotor cortex and corticospinal tract (Jenner & Stephens, 1982).

Another methodological approach to assess the use of peripheral feedback in the control of movement is to examine the phase dependency of the reflex response to various stimuli during cyclical movements. Modulation of the H-reflex, cutaneomuscular reflex and stretch reflex elicited in leg muscles has been extensively studied in this way during locomotory behaviours in both animal and human subjects (Forssberg, Grillner & Rossignol, 1975, 1977; Kanda & Sato, 1983; Schieppati, 1987; Dietz, 1992; Stein, 1995). However, phase-dependent reflex responses have been very little investigated in the human upper limb. Very little attention has been paid to rhythmic voluntary movements of the hand in either normal subjects or patients with motor disorders, with some exceptions (e.g. Freeman *et al.* 1993; Adamovich, Levin & Feldman, 1994; O'Boyle, Freeman & Cody, 1996).

Handwriting: rhythmical hand movement

A historical review of handwriting

The following short introduction to the fascinating history of the development of handwriting was based on a book “*The Story of Handwriting: Origins and Development*” written by Alfred Fairbank (1970) which describes and illustrates the evolution of handwriting fully, and a book “*Developing Handwriting*” by Peter Smith (1977) which summarises the main trends of the former book.

Handwriting has been gradually evolving as civilisation progresses. The first people who developed a full system of written language were the Sumerians. They used a monosyllabic system developed from simple pictograms and ideograms about the year 2500 BC. During that time, a triangle-shaped reed used as the stylus resulted in the change from curved to straight lines. The available materials may influence the writing style of the time.

Research and discoveries, particularly in the caves of Spain and France, have revealed that the beginning of recorded communication was in the form of pictures painted on the walls of caves. From these first pictures early man developed picture

writing which he may have used as an aid to memory or as a record of a transaction. These pictograms were simple drawings of a significant part of an object and were used to represent the whole.

The ancient people considered the ability of writing so remarkable that they attributed magical or religious qualities to those who possessed the skill. The early Egyptians believed that the gods Thoth and Isis gave them the knowledge of writing, whereas the Babylonians gave credit to Nebo, the Greeks to Hermes and the Hindus to Brahma. Moreover, the father of Chinese writing, Ts'ang Chieh, was thought to be so perceptive that he had been endowed with an extra pair of eyes.

The Ancient Egyptians used three kinds of scripts. From the year 3000 BC or so until the time of Christ, they used the 'hieroglyphic' style which was mainly used for inscriptions on buildings and monuments and consisted of simplified formalised pictures in vertical columns carved on stone. However, out of this evolved the 'hieratic' style which developed due to two particular circumstances: the first was the invention of papyrus which made it possible to write with brush or reed pen and thus faster and with less restriction; the second was the change from writing vertically to horizontally, from right to left. The third style of writing used by the Ancient Egyptians, called 'demotic', first appeared about the year 700 BC. It was a rapid, fluent, cursive style and was a departure from the pictorial quality of hieroglyphics.

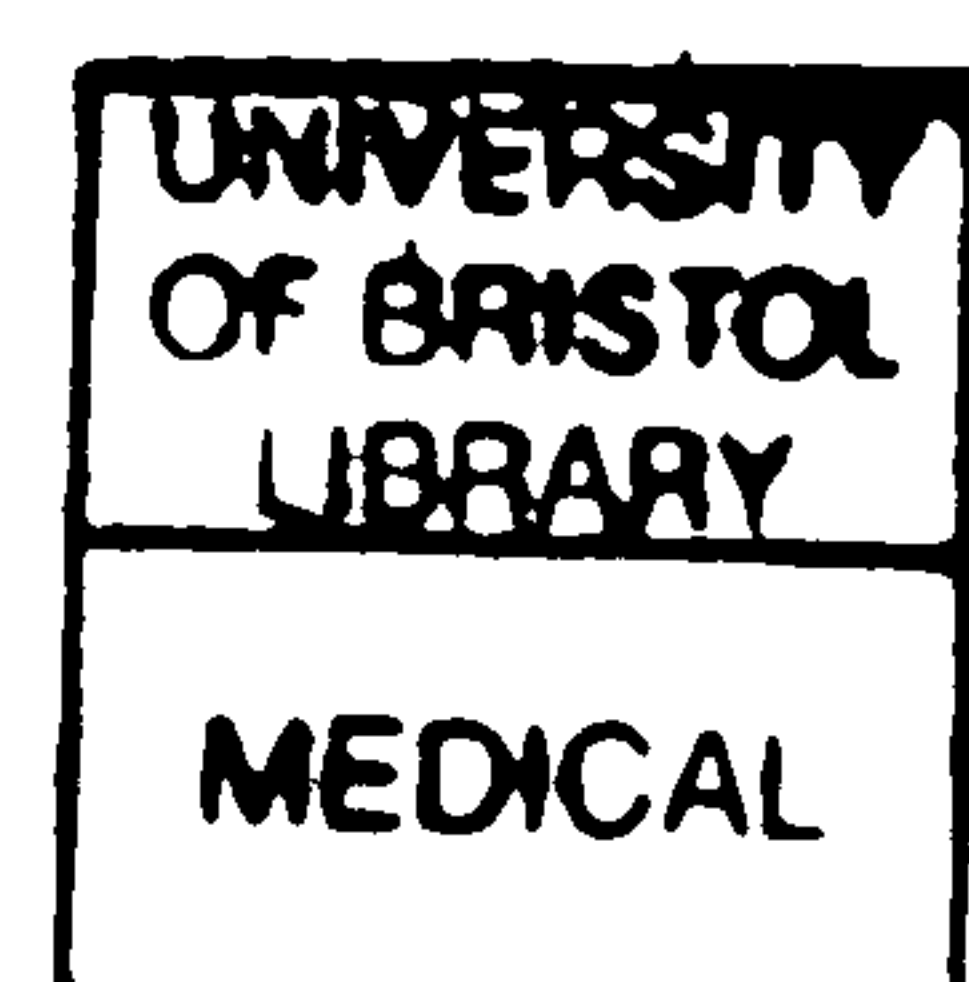
The written languages of modern Western civilisations are based on a collection of symbols called letters which are written to represent the sounds used in speech. It is not known who invented the very first alphabet and precisely when it was invented. However, historians do suggest that Byblos was the place where it may all have begun. An alphabet of twenty two letters was used in the inscription on the sarcophagus of King Ahiram of Byblos and is believed to have been carved in the eleventh century BC. The Phoenician alphabet, which was influenced by Egyptian writing, was developed from the Semitic alphabet of Byblos. It also comprised twenty two letters, but none of them

was a vowel. The first two letters were named as “aleph” and “beth”. The Greeks then adapted the Phoenician alphabet by adding vowels. They named the first two letters “alpha” and “beta”. The word “alphabet” was derived from these two names. The Greeks also changed the direction of horizontal writing from left to right, which is much more convenient for a right-handed person.

The alphabet we use today follows very closely the one which the Romans developed in the centuries immediately preceding the birth of Christ. It was based on the framework acquired from the Greeks. An excellent example of the proportion and grace of the Roman alphabet is the capital letters forming the inscription at the base of the Trojan column in Rome, which served as the model for our present printing type. The Roman alphabet consisted of only capital letters. By the sixth century AD, scribes had evolved an alphabet of half-uncials. These are generally known as the “small” letters, but are better called the “lower-case” letters since any symbol may be written large or small in size. The term “lower-case” is derived from the practice of arranging the compositor’s type in two sets of cases. The less-used capital letters are kept in the upper cases while the more frequently needed “small” letters are stored in the lower cases.

As well as the formal scripts used in the writing of books there were cursive scripts also based on the half-uncials, which developed in the course of the informal writing used in correspondence and in personal note-taking. The first “Italic” hand is thought to have been invented by a Florentine scholar called Niccole Niccoli who made use of diagonal joins and up-strokes as he wrote at speed avoiding pen-lifts. He also altered the shapes of some letters and changed proportions of others.

The pen used for writing was the goose quill (the name ‘pen’ deriving from *penna* which is Latin for feather). The quill was cut by the scribe himself and was given a broad tip for longer wear. Such a nib gives rise to the characteristic thick and thin strokes without need for variation in pressure. It also became accepted that writing with



the pen held at an angle of forty-five degrees to the line of writing enabled the scribe to write faster and to fit more words on to a line.

Different postures of holding a pen in handwriting

Handwriting, human's highest manipulative skill, requires highly co-ordinated motor performance of a large number of hand muscles. Like locomotion, handwriting also involves repetitive movement. Around 1895, Wilhelm Preyer, a professor of psychophysiology, demonstrated that handwriting is generated by the brain. Recent studies indicated that handwriting is regulated by morphokinetic and topokinetic components. The morphokinetic components refer to the cursive trajectory forming letters and are generally produced automatically. Research on handwriting also suggests that letters are written by concatenating morphokinetic components. On the other hand, the topokinetic components refer to the displacements of the hand within the constraint of a graphic space.

Holding a pen may be considered as a kind of either power or precision grip, which is performed either by the whole hand or between thumb, index and middle fingers, even other fingers as well. The number of the fingers involving the grip depends on the posture of holding a pen. On the basis of a review of the literature, ten types of grip were differentiated (Schneck & Henderson, 1990; Schneck, 1991): (1) radial cross palmar grasp; (2) palmar supinate grasp; (3) digital pronate grasp; (4) brush grasp; (5) grasp with extended fingers; (6) cross thumb grasp; (7) static tripod grasp; (8) multiple finger grasp (four or five finger grasp); (9) lateral tripod grasp; (10) dynamic tripod grasp. These grips are given in developmental order and illustrated in Figure 1.3. The earlier ones are more like the power grip and the later ones like the precision grip. In order to achieve efficient writing, intrinsic and extrinsic hand muscles have to work in good co-ordination to produce the appropriate biomechanical forces involved in maintaining smooth writing. This requires several fingers to move together rather than the independent movement of an individual digit. Therefore, handwriting is one of the most complex finger manipulations combining gripping with dynamic finger

movements. Normal cursive handwriting appears to be a combination of loops and vertical, horizontal and oblique lines drawn on a planar surface. Due to the complexity of handwriting, a series of simple, stereotyped movements (e.g. drawing a vertical or horizontal line, a circle or an oval) representing handwriting, were performed in this study. The detailed information about these handwriting movements will be described in Experimental protocol of Chapter 3 or 4.

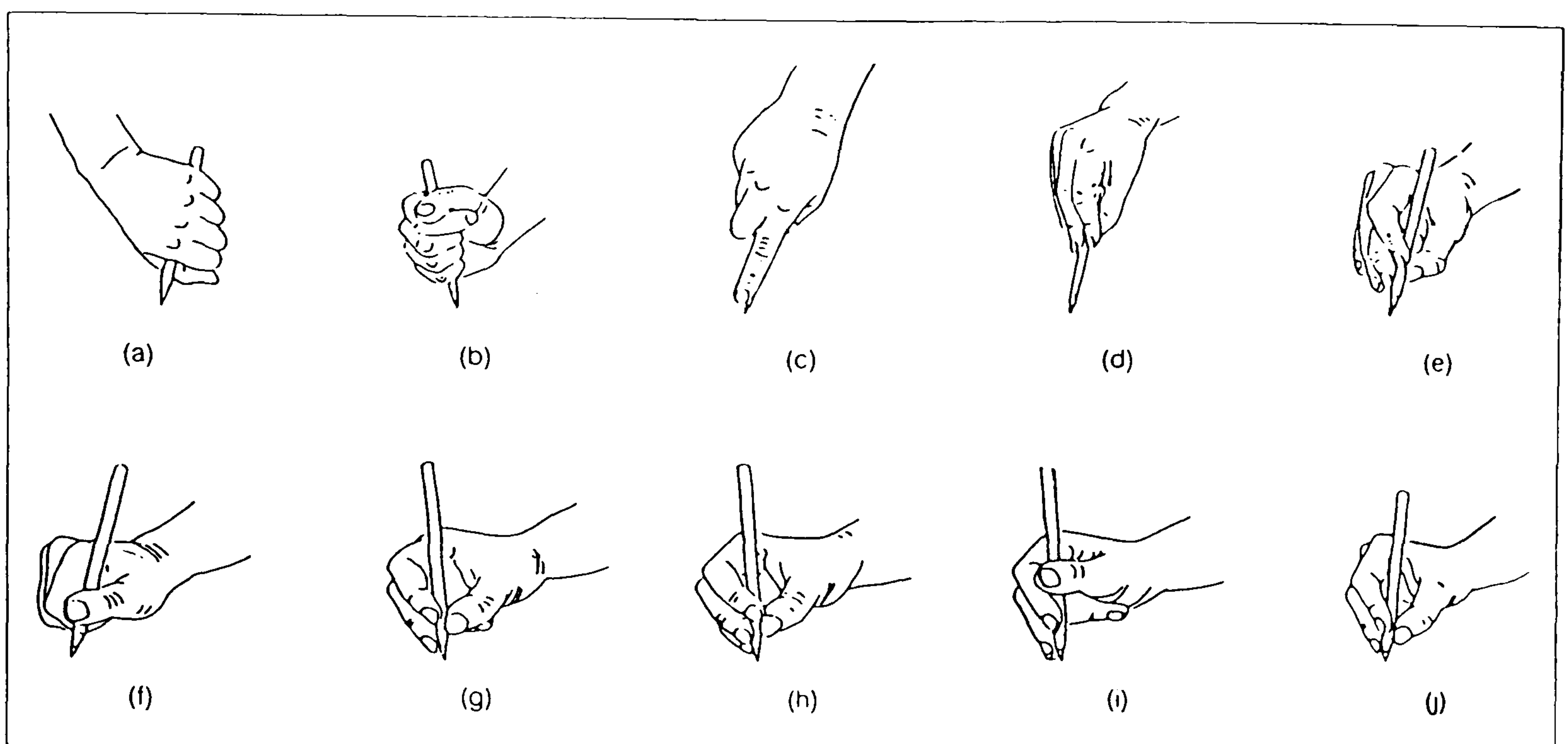


Figure 1.3. Operational definitions of grip posture in developmental order: (a) radial cross palmar grasp; (b) palmar supinate grasp; (c) digital pronate grasp; (d) brush grasp; (e) grasp with extended fingers; (f) cross thumb grasp; (g) static tripod grasp; (h) multiple finger grasp (four or five finger grasp); (i) lateral tripod grasp; (j) dynamic tripod grasp. (From Schneck & Henderson, 1990).

With the advent of computers, it is now common to write using word processing packages. Nevertheless, handwriting is still of great importance in our daily life and its usage cannot be neglected. Despite a considerable body of work involving the study of handwriting, the muscle co-ordination patterns during repetitive finger movements or handwriting have not hitherto been examined. Furthermore, comparisons have never been made between the muscle activity patterns of different pen-grips during discrete writing tasks and handwriting.

Writer's cramp

Writer's cramp has been recognised for at least a century and a half. It was originally perceived to be a physical motor disorder. In recent years, evidence has accumulated to show that writer's cramp is a real focal motor disorder, with a close relation to dystonia (Marsden & Sheehy, 1990). Whether writer's cramp is a physical disorder or a true focal dystonia of the hand continues to be debated. Yet, the cause of writer's cramp and its pathophysiology remain unknown.

A typical writer's cramp may present the common features of elevation of the elbow, hyperpronation of the forearm, and forced grip of the fingers on the pen. In some cases, sudden jerks and tremor during writing may occur. Electromyographic investigations (Rothwell *et al.* 1983; Hughes & McLellan, 1985; Sheehy, Rothwell & Marsden, 1988) have shown that instead of the normal alternating contraction of agonist and antagonist muscles, patients with writer's cramp show co-contraction. In addition, there is difficulty in selecting the appropriate muscles to carry out manual tasks.

Due to the difficulties in recruiting subjects with writer's cramp, this study was mainly concentrated on subjects exempt from any neurological disorders. A small number of volunteers who suffered from writer's cramp did participate in the experiments, but not in sufficient numbers to draw any definitive conclusions. Nevertheless, some of the results obtained from writer's cramp subjects will still be presented here in Chapter 6, as it may be of interest for future research.

Purpose of this study

The function of movement has been developing and improving with evolution. Generally, movement can be classified into three main types: reflex movement, voluntary movement and rhythmic movement. Reflex movement is the simplest, most basic and stereotyped movement. The execution of a voluntary movement involves a few stages: (i) idea; (ii) motor plan; (iii) execution of programme commands; (iv) move.

Rhythmic movements, like breathing, chewing and locomotion, are generally accepted to be controlled by pattern generators in the brainstem or spinal cord. As an example of a rhythmical manual task, writing involves co-ordinated spatial and temporal patterns of activity in many muscles controlled by central “motor programmes” and sensory feedback from peripheral proprioceptors. Although rhythmic actions have been extensively studied in leg muscles for over a century, little is known about hand muscle behaviours while performing repetitive movements, especially handwriting -- one of the highest skilled movements in humans.

In this study, three main objectives have been addressed:

- (1) to identify characteristic co-ordination patterns of different hand muscles during the performance of a range of rhythmic manipulatory tasks representing different components of handwriting;
- (2) to compare the patterns of hand muscle activity in individuals who use the standard dynamic tripod grip (DTG) and those who employ unusual pen grips, such as, four finger grasp (4FG) and five finger grasp (5FG), for both right- and left-handed subjects, during component writing;
- (3) to assess the role of proprioceptive feedback by examining phase-dependent reflex responses evoked by mechanical or electrical stimulation applied at different phases of repetitive finger movements related to handwriting.

The general method employed in this study included recording the surface electromyographic activities simultaneously from four of six selected hand and forearm muscles, along with some monitor signals which also serve to identify the beginning and end of each cycle. This was carried out during handwriting and other prescribed manipulative tasks and rhythmic movements of the fingers. This technique has been traditionally used in physiological studies. However, the method used to analyse the EMG activity during rhythmic movements was developed during the course of this study and has been published in abstract form (Xia & Bush, 1996b). The procedure of this data analysis is given in Appendix 1.

In this thesis, the General Introduction (Chapter 1) is followed by Materials and Methods (Chapter 2) describing those methods that are common to several of the experiments. Chapters 3 to 5 each deal with separate series of experiments. Chapter 3 focuses on the motor co-ordination patterns of different hand muscles during rhythmical finger movements representing handwriting. Chapter 4 discusses the characteristic differences of muscle activity displayed by those employing the standard or uncommon pen-grips. Chapter 5 addresses the modulation of reflex responses during cyclical finger movements related to handwriting. Chapter 6 reflects the voluntary movement and reflex behaviour of hand muscles during prescribed movements in writer's cramp subjects. These are followed by a General Discussion (Chapter 7), one Appendix and the Reference list.

CHAPTER 2

MATERIALS and METHODS

Subjects

Fifty four healthy subjects (30 males, 24 females) and two writer's cramp subjects (2 males) participated in this study, which had been approved by the Local Ethical Committee. The mean age of the normal subjects was 28 ± 11 (SD) yrs, ranging from 18 to 65 yrs, and the age range of two writer's cramp subjects was 19 to 62 yrs. Within the normal group, forty two subjects were right-handed dominant and twelve left-handed. Both writer's cramp subjects were right-handed dominant, but one had started to write with his left hand after some time of self-training. Other subjects have no history of neurological disorders. Informed consent was obtained from each subject before participating in the experiment. Three series of experiments were conducted in this study, and some subjects took part in more than one experiment.

Anatomical structure of muscles studied

Six muscles were selected for the recording of EMG activity in this study. These included three intrinsic hand muscles: flexor pollicis brevis (FPB), abductor pollicis brevis (APB), 1st dorsal interosseous (1DI) and three extrinsic hand muscles in the forearm: flexor digitorum superficialis (FDS), extensor digitorum communis (EDC) and extensor pollicis brevis (EPB). These muscles were selected for this study for two reasons: they are accessible and superficially located, and are therefore easily detected by surface electrodes and do not require invasive procedures to establish a clear EMG signal; they are the muscles most relevant to hand manipulative tasks and handwriting. These muscles are commonly used as representatives of the active flexor musculature during hand-grip manoeuvres. Muscles FPB and EPB are one pair of agonist and antagonist to the metacarpophalangeal joint of the thumb. FDS and EDC act as finger flexor and extensor, which are another pair of agonist and antagonist muscles. 1DI is involved in very fine manipulative skills and has been extensively studied by many researchers.

In order to locate each muscle properly, it is necessary to elucidate the anatomical structure of each muscle recorded in these experiments. Intrinsic muscles of the hand are divided into three groups (Spencer & Mason, 1992). Those that act on the thumb form the thenar eminence at the base of the thumb. Those that act on the little finger form the hypothenar eminence on the medial side of the hand. The intermediate, or midpalmar, muscles act on all the phalanges except the thumb. The origin and insertion of intrinsic muscles are both in the hand. The intrinsic muscles make possible the fine and precise movements that are typical of the fingers. Muscle FPB belongs to the thenar muscle group. This muscle flexes the thumb at the metacarpophalangeal joint, and assists in abduction and rotation of the thumb. Its origin is on the flexor retinaculum, trapezium and first metacarpal bone. Its insertion is on the base of the proximal phalanx of the thumb. It is innervated by median and ulnar nerves. Thenar muscle APB abducts the thumb and moves it anteriorly. Its origin is on the flexor retinaculum, scaphoid and trapezium, and its insertion is on the proximal phalanx of the thumb. The innervation to APB muscle is via the median nerve. The 1st dorsal interosseous is one of the midpalmar muscles of the hand. 1DI abducts the index finger away from the middle finger at the metacarpophalangeal joint. 1DI has two heads originating from adjacent sides of the first and second metacarpal bones, and has its insertion at the lateral side of the proximal phalanx of the index finger. This muscle is innervated by the ulnar nerve.

Extrinsic forearm muscles that act on the hand and fingers can be divided into two groups on the basis of location and function. The muscles of the anterior group serve as flexors or pronators. The posterior group of forearm muscles serve as extensors and supinators. FDS is one of the superficial muscles on the anterior surface of the forearm. Its main action is to flex the fingers at the proximal interphalangeal joint (PIP joint). The origin of the humeroulnar head is at the medial epicondyle of the humerus through a common tendon, and the medial margin of the coronoid process of the ulna. The origin of the radial head is at the anterior surface of the shaft of the radius. Four tendons of FDS divide into two slips, each inserting into the sides of the middle

phalanges of the four fingers. FDS is innervated by the median nerve. EDC is located on the posterior surface of the forearm and extends the fingers and the hand. Its origin and insertion are the common tendon attached to the lateral epicondyle of the humerus, and the lateral and dorsal surfaces of all the phalanges of the four fingers. The innervating nerve is the deep branch of the radial nerve. EPB is located on the deeper layer of the posterior group of muscles and acts mainly as a thumb extensor. Its origin is at the posterior surface of the radius, and the adjacent part of the interosseous membrane, and its insertion is at the base of the proximal phalanx of thumb. It is innervated by the radial nerve (Stone & Stone, 1990). The origins and insertions of these six muscles and adjacent structures are illustrated in Figure 2.1.

Experimental apparatus

Force pens

Two force pens were subsequently used in this study to measure the forces exerted by the thumb and four fingers, and were also employed to identify the onset time of each movement cycle. One of them, with strain gauge on one side, was used in Experiments I and II (see Chapters 3 and 4: Experimental Protocol), and the other one, with strain gauges on three sides, was used in Experiment III (see Chapter 5: Experimental Protocol). Both one-way and three-way force pens worked in the same principle. The three-way force pen enabled the forces experienced along three axes, 120 degrees apart and perpendicular to the long axis of the pen, to be independently measured. A standard ball point pen refill was housed in a brass hexagonal tube. The tube had been machined to produce three flexible beams equally spaced around the circumference of the tube. A foil strain gauge was bonded onto the top surface of each beam, and each gauge was electrically connected as one arm of a bridge. A regulated excitation voltage was applied to each bridge and the output signals from each transducer were suitably amplified, level shifted and filtered before connection to a Cambridge Electronic Design (CED) 1401 interface.

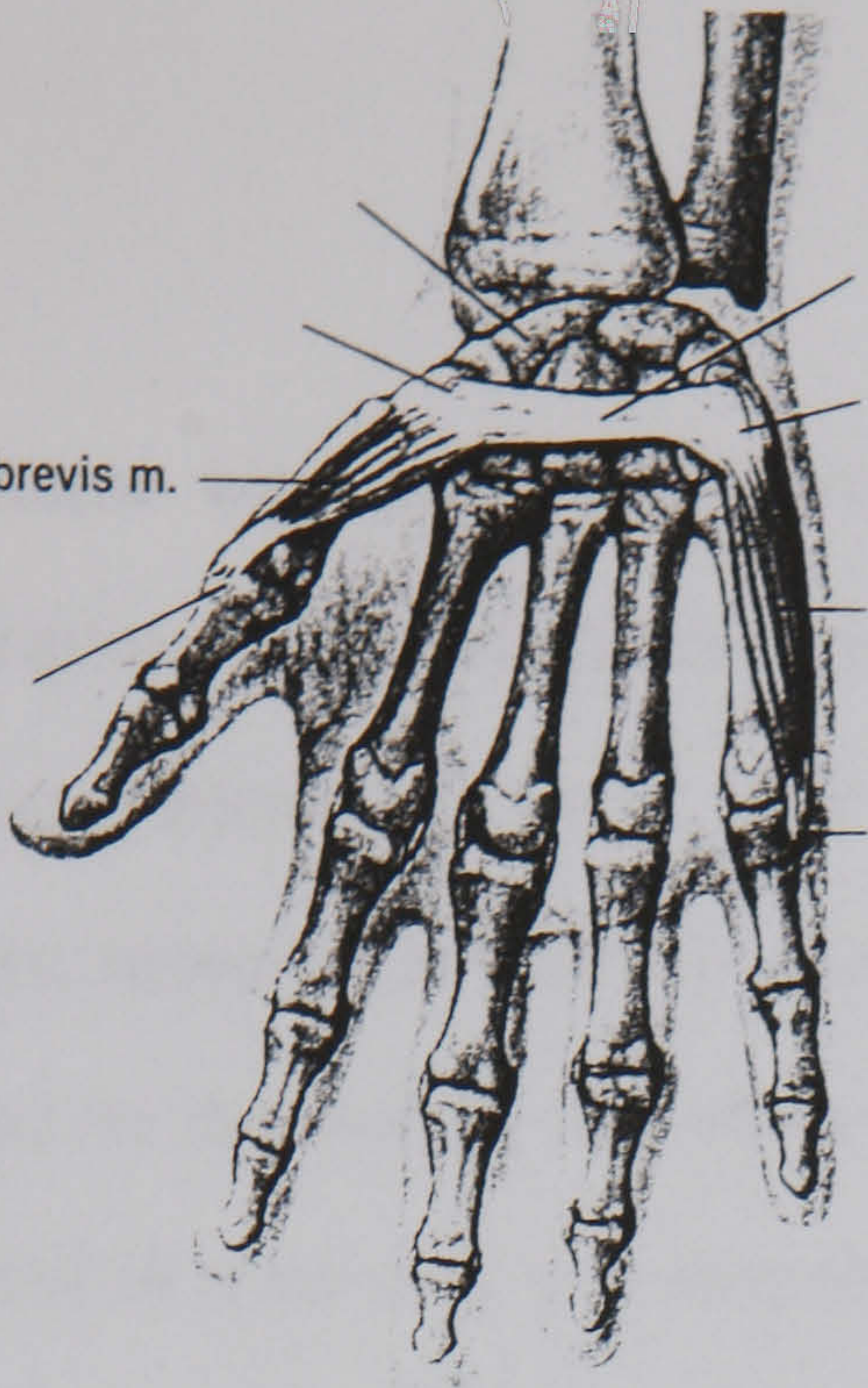
Figure 2.1. Diagrammatic illustration of six muscles selected for this study.

<i>A</i> : abductor pollicis brevis (APB);	<i>B</i> : 1st dorsal interosseous (1DI)
<i>C</i> : flexor pollicis brevis (FPB);	<i>D</i> : extensor pollicis brevis (EPB)
<i>E</i> : flexor digitorum superficialis (FDS);	<i>F</i> : extensor digitorum communis (EDC)

(Modified from Olson, TR: *A.D.A.M. Student Atlas of Anatomy*. 1996, Williams & Wilkins, Baltimore, MD.)

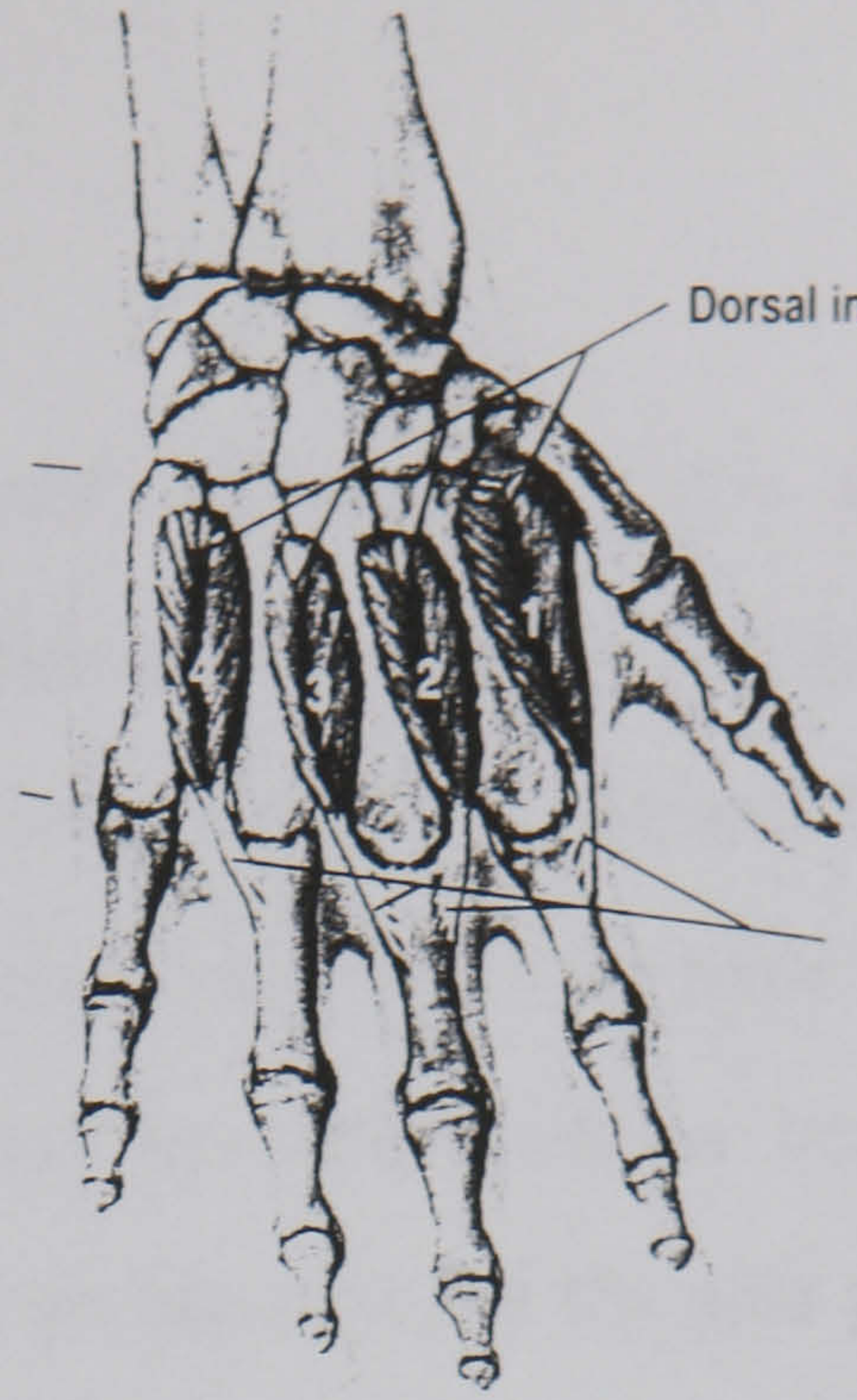
A

Abductor pollicis brevis m.



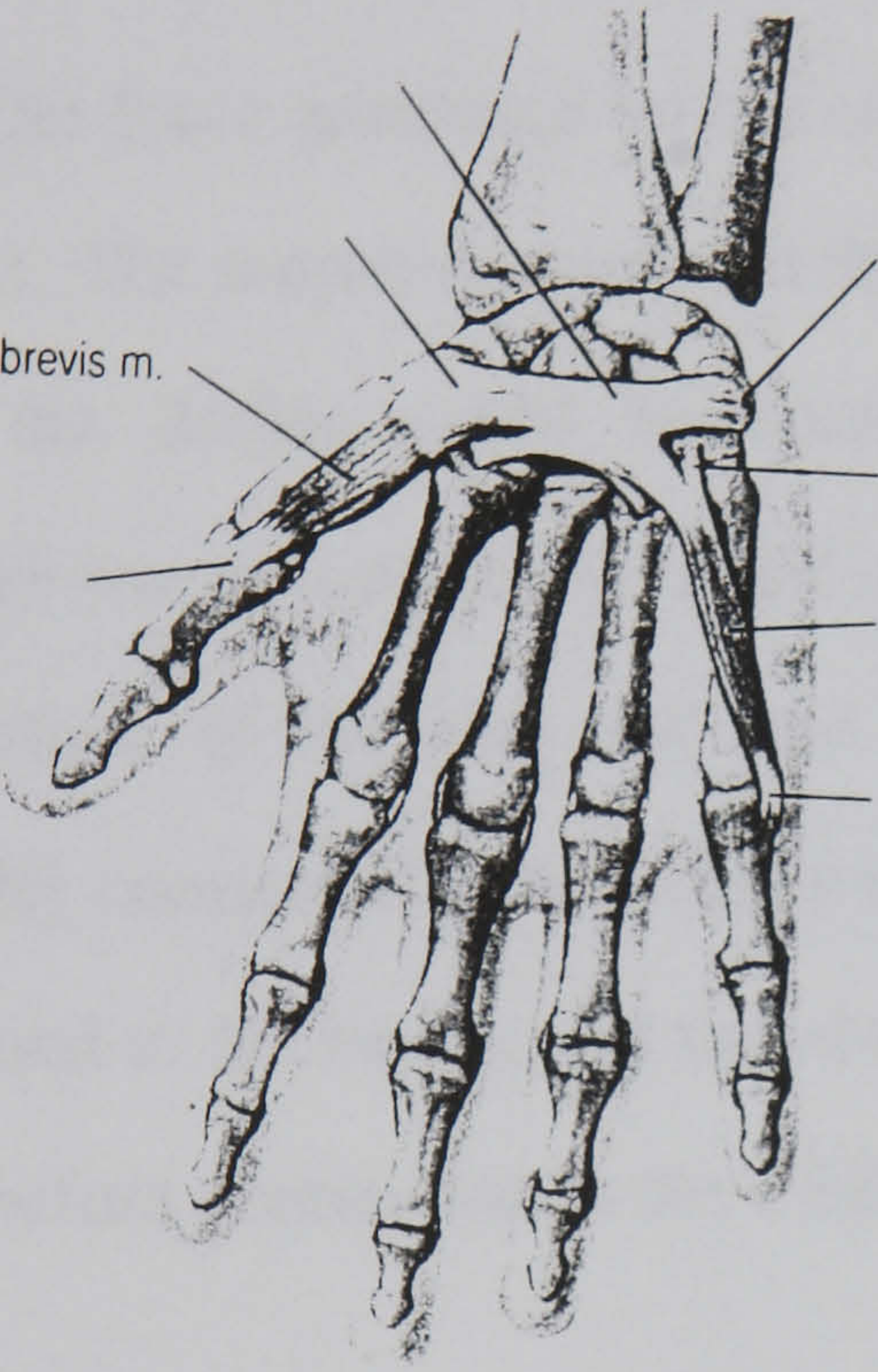
B

Dorsal interosseous mm.



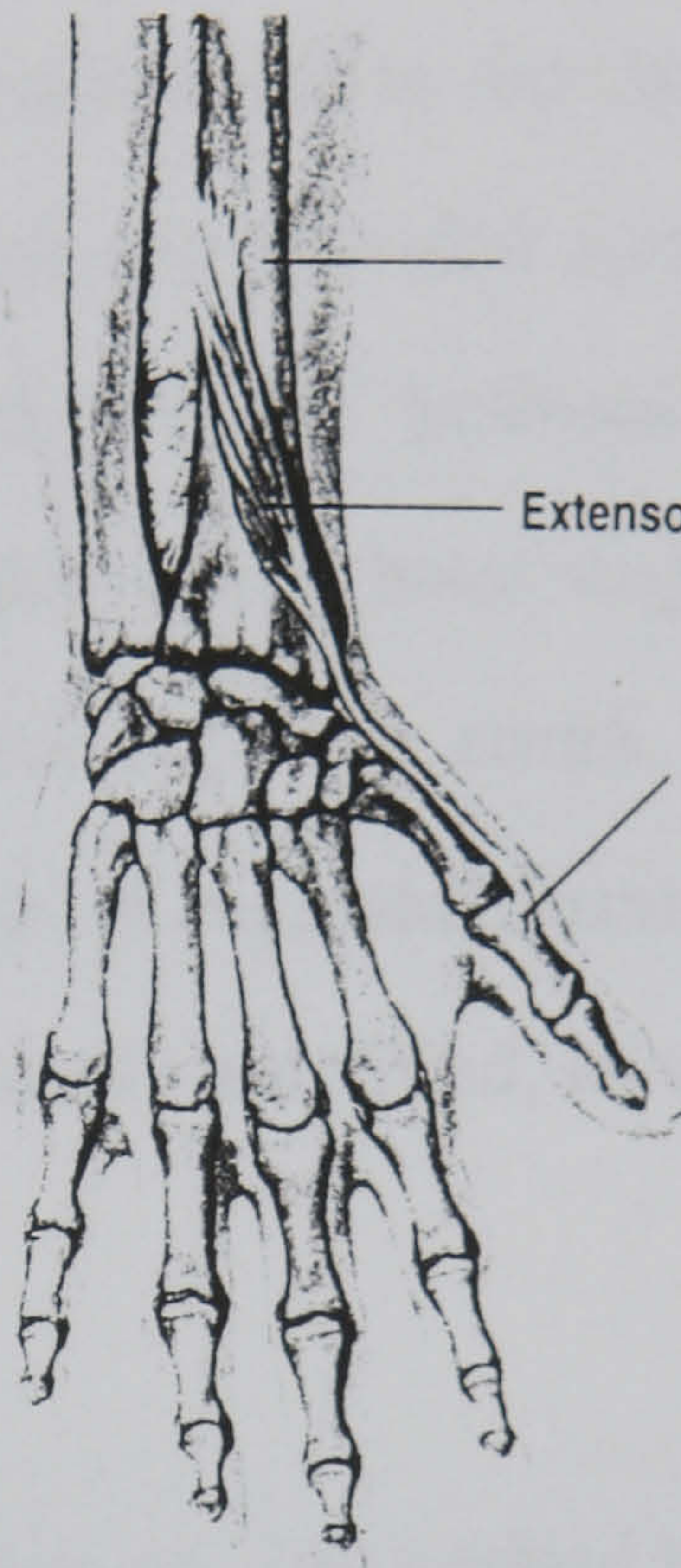
C

Flexor pollicis brevis m.



D

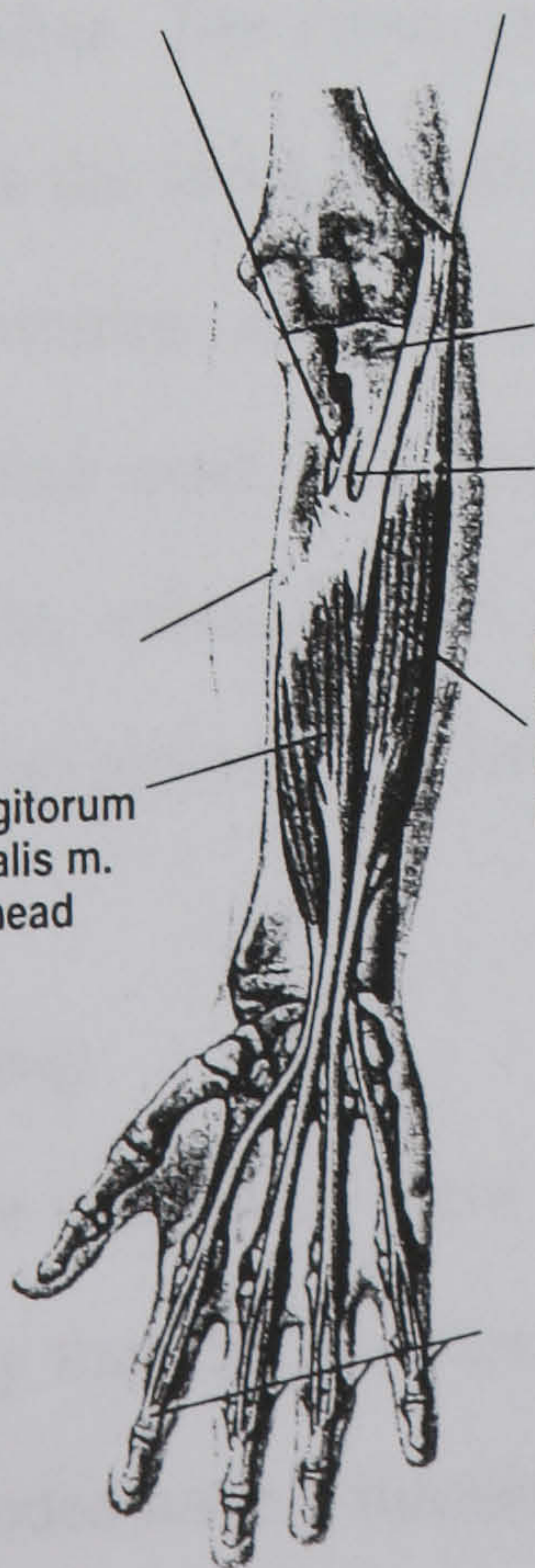
Extensor pollicis brevis m.



E

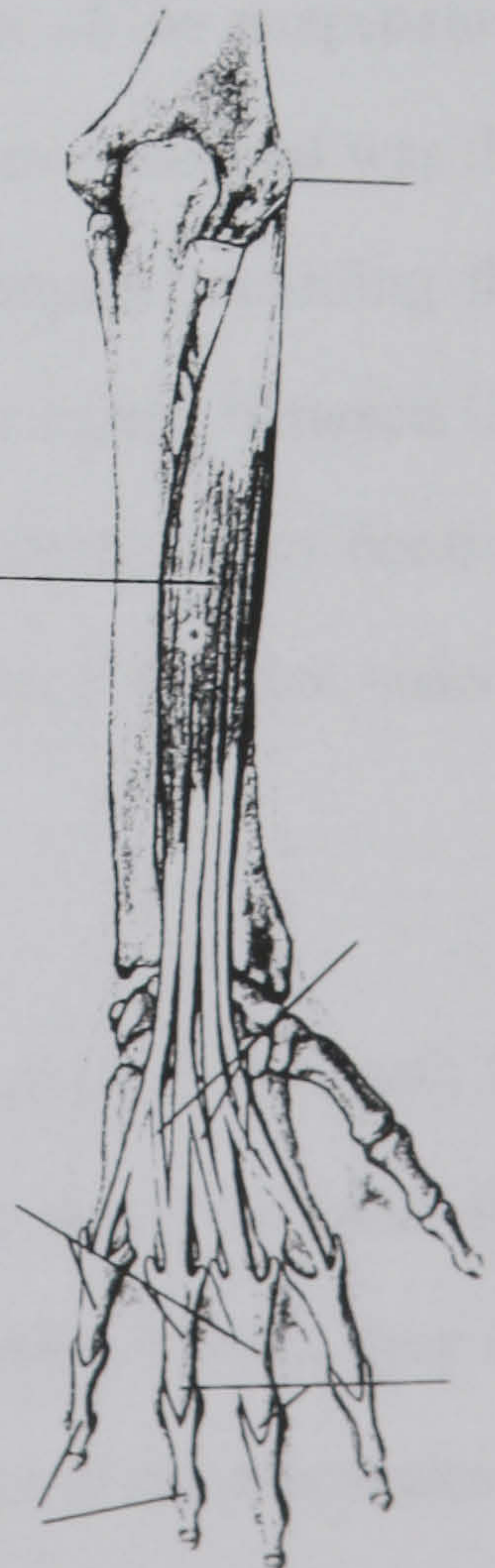
Flexor digitorum superficialis m.—radial head

Flexor digitorum superficialis m.—humero-ulnar head



F

Extensor digitorum m.



Vibrator

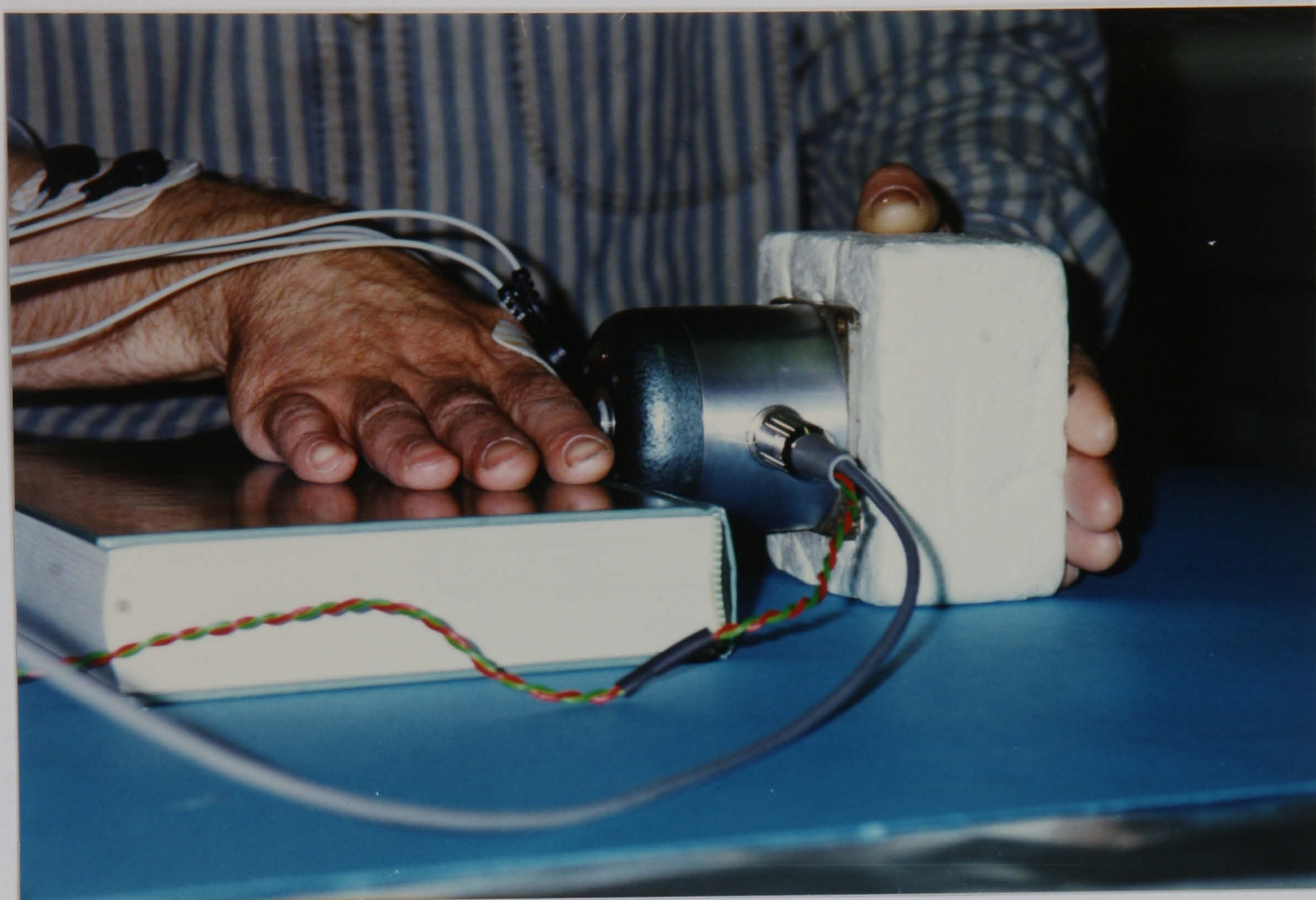
A vibrator was used to produce mechanical stimulation in this study. The detailed description of the application of the mechanical stimulation will be given in Chapter 5: Experimental protocol. The vibrator, or prodder, was essentially a linear electromagnetic motor (Pye-Ling) in series with a force transducer. The force transducer was connected to the output rod which was located by a PTFE sleeve bearing. The motor consisted of a moving coil suspended in the air gap between the pole pieces of a permanent magnet. The arrangement was the same as that employed in loudspeaker design. The force generated by the coil was directly proportional to the current flowing through it. The suspension located the coil in the air gap and provided a restoring force so that the device could be conveniently operated without feedback. The force transducer was formed by four foil strain gauges bonded onto a brass ring, two on the inner surface of the ring and two on the outside surface. The strain gauges were electrically connected as a bridge with four active arms. A regulated excitation voltage was applied to the bridge and the output signal was suitably amplified, level shifted and filtered before connection to the CED 1401 interface.

A signal from a pulse generator or function generator was applied to the coil via a power amplifier. The force generated, minus the restoring forces of the suspension, was applied via the force transducer to the pen-tip or finger. The force measured was the sum of the stimulus and the forces generated by the hand and fingers including the effects of inertial mass. The displacement produced by the prodder varied between 0.5 and 1 mm. The vibrator used in this study is run open-loop, without servo control. Figure 2.2 shows the vibrator being used in the experiment during three different tasks.

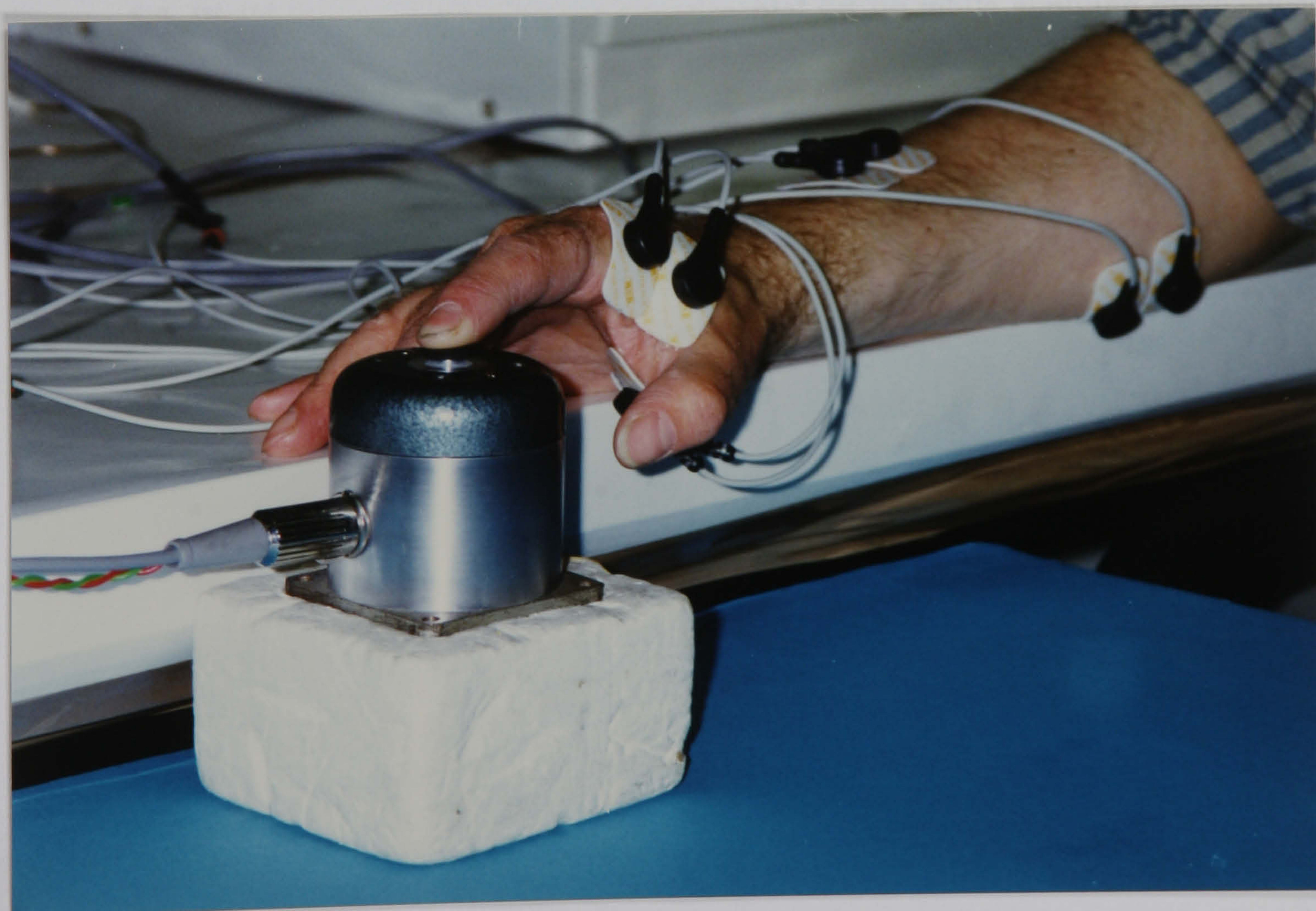
EMG recording

Surface electrodes were used for all EMG activity in this study. The reason for this is not only that the muscles being investigated in this study are superficial, but also surface electrodes have a number of advantages over needle electrodes. Firstly, they did not cause any discomfort to the subject, either during the application of the electrodes or

A



B



C

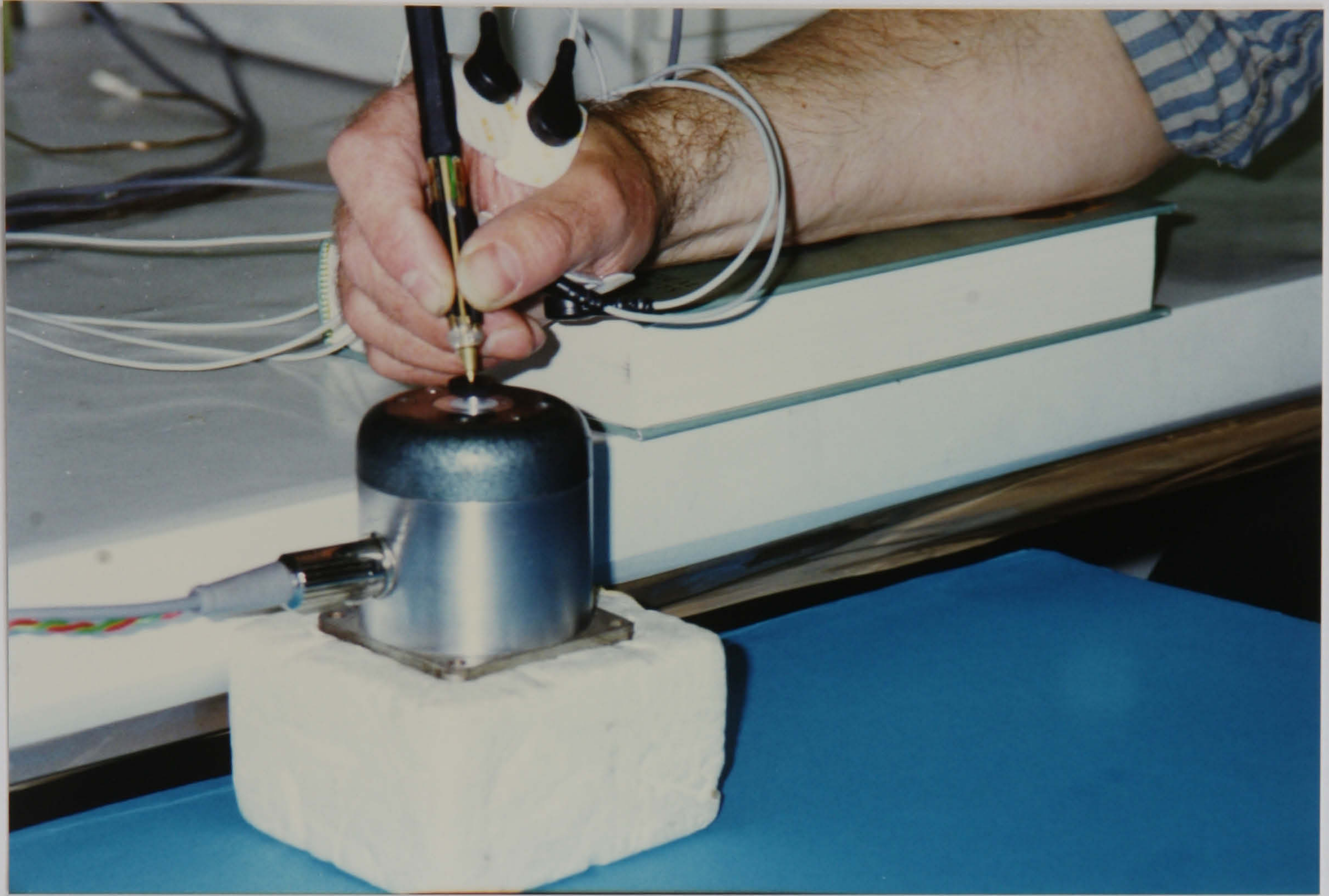


Figure 2.2. Photographs illustrating the experimental set-up while applying mechanical stimulation during the three tasks (see Chapter 5: Experimental protocol for detail). A: finger abduction (task 1); B: finger press (task 2); C: pen-tip (task 3).

subsequently. Secondly, the mean level of the rectified EMG is approximately linearly related to muscle tension under isometric conditions (Lippold, 1952) or contraction at constant velocity (Bigland-Ritchie & Lippold, 1954). Thirdly, surface electrodes can be easily and quickly applied in the absence of medical supervision. Finally, the amplitude of surface EMG activity recorded from a particular muscle under certain test conditions is far more repeatable than EMGs obtained with needle or wire electrodes (Jonsson & Komi, 1973). A possible disadvantage, however, is the occasional presence of some cross talk while recording EMG from small muscles. Taking all these reasons into account, therefore, surface electrodes were selected for this study, particularly since EMG activities occurring simultaneously in a number of muscles were being investigated.

EMG activities were usually recorded simultaneously from four of the following six muscles: FPB, APB, 1DI, FDS, EDC and EPB which have been described earlier in this Chapter. The skin areas over each recorded muscle were gently abraded using special skin preparation pads (Biolect, UK) in order to reduce the resistance between the reference and recording electrodes. Skin was then cleaned with Ethanol 95 to remove surface grease and was allowed to dry completely. For each subject, surface EMG recordings were obtained using a pair of 9 mm diameter Ag-AgCl bio-adhesive electrodes (Biotrace, UK), 2 cm apart, attached to the skin over the belly of each of the investigated muscles.

The recordings were bipolar, with an inter-electrode spacing of approximately 2 cm longitudinally. The proximal electrode was placed over the belly of muscle and the other one was placed more distally, close to the muscle tendon in the intrinsic muscles. A reference electrode was positioned over the sternum. Four pairs of electrodes and the reference one were connected into an isolated preamplifier, the proximal electrode being linked to the positive terminal and the distal one to the negative terminal, and the reference electrode to the earth. Before the recording session began, the placement of the electrodes over each muscle was checked by observing the EMG activity displayed

on an oscilloscope during rapid alternating contraction and relaxation of each muscle. For example, when checking FPB electrode placement, the subject was asked to perform alternating flexion and extension of the proximal phalanx of the thumb, while the EMG signal was observed on the screen of the oscilloscope for confirmation. The EMG signals from each of the four muscles were amplified $\times 10$ gain by the isolated preamplifier. Signals were then fed into additional amplifiers for a further $\times 100$ amplification in parallel and were band-pass filtered (bandwidth 10 Hz - 5 kHz) before sampling at a rate of 2000 Hz per EMG channel through the 1401 interface, as described previously (Xia & Bush, 1995, 1996a). Digitised signals were stored onto a Viglen *genie* *PCi* computer for subsequent analysis. In addition, the force signals used to monitor each movement cycle were also recorded simultaneously.

Experimental procedure

General procedure comprises three series of experiments which will be described separately. Muscles being recorded and tasks performed varied in different experiments depending on the objective of each study as addressed in Chapter 1. Protocols related to Experiments I to III will be given in Chapters 3 to 5, respectively.

Data analysis

EMG data stored on computer disk were replayed and analysed off-line. Raw EMGs recorded from all experiments were first fullwave rectified, and low-pass filtered for the EMGs recorded from Experiments I and II only. EMGs were then averaged between cycles with respect to phase, or averaged time-locked to the stimulus for Experiment III.

Identification of movement cycle

Analysis of rhythmic activity required identification of onset and offset of each cycle. The way to identify the onset of the movement cycle depended on the task. For tasks 'vertical writing' (VW) and 'horizontal writing' (HW) in the Experiments I and II (see Chapters 3 and 4: Experimental protocol), the output of a linear potentiometer was

recorded as a ramp waveform to monitor these two movements, and the onset of each cycle was defined as the bottom edge of the ramp. During 'oval writing' task (see Chapter 4: Experimental protocol), when the pen-tip contacted the wire, a pulse was produced so that the onset of each movement cycle could be recognised on the basis of the pulse signal. In handwriting tasks, the onset of cycle was identified in a similar way to the 'oval writing'. For other movements, rectified and low-pass filtered EMG signals were visually inspected to determine the starting time of the EMG burst in one muscle, which was taken as the onset of the movement cycle. EMGs were averaged over at least 10-15 movement cycles so that the modulation patterns of muscle activity can be investigated for various tasks.

EMG signal phase average

Following identification of the movement cycle, each cycle period is divided into an equal number of subdivisions (N). The width of each subdivision thus depends on the duration of each cycle, which may vary somewhat with self-paced cycles, even when the frequency depends upon a pre-set 'metronome' frequency. The mean EMG amplitude within each subdivision is computed. The same computation was applied to the subdivisions of every cycle. These EMG means for each sequential subdivision over all the successive movement cycles in a task are then averaged to produce the final phase average diagram. Averaged EMG signals are then plotted on a normalised time-base or called phase, with the vertical axes showing either the actual EMG amplitude or the amplitude normalised to the maximal value for each muscle (Xia & Bush, 1996b). The procedure is described and expressed using the matrix and formula given in Appendix 1.

Phase diagrams were constructed by averaging EMGs over 10-15 cycles normalised with respect to phase for each subject. In general, the amplitude of muscle activity between subjects from the same group was consistently modulated. Comparisons were made between groups according to handedness or pen-grip and so on by plotting the phase diagram in the form of mean \pm s.e.m. between the same group subjects.

Measurement of reflex responses

In Experiment III (see Chapter 5: Experimental protocol), the EMGs were full-wave rectified and were then averaged in relation to the stimuli over several steps. Each cycle was separated by the trough of sinusoidal force signal produced by the index finger from the prodger during tasks ‘finger abduction/adduction’ and ‘finger press’ or from the force pen during task ‘pen-tip’. To examine the dependency of the reflex responses on the phase of the above rhythmic movements, each movement cycle was then divided into eight or sixteen equal parts (phases). All responses occurring within the same phase were grouped and averaged together (Akazawa *et al.* 1982; Yang & Stein, 1990). Typically, one 3-min run consisted of a total number of approximately 260 stimuli. Generally, an approximately equal number of stimuli were obtained in each phase over the cycles.

The latency of reflex responses was determined by visual inspection of rectified, averaged EMG with the aid of a cursor on the computer screen. It was measured as it intersects the mean background EMG level (a 20 ms EMG average before the stimulus). The latency generally did not vary over the movement cycle from each muscle for each subject. The same latency was therefore used to calculate the amplitude of the responses in all parts of the movement cycle.

The duration of each average trace was 120 ms starting from stimulus, which was sufficient to cover all reflex components. The amplitude of the response under static state was defined as the difference between the average EMG over the specified window and the background EMG level. The window was specified as the duration between intersection points of response and background level. Under dynamic conditions, the response to the stimulus was superimposed on the normal undisturbed movement. To obtain an estimate of the reflex component alone, the undisturbed pattern of muscle activity was subtracted from the stimulated recording. The size of the response was thus measured as the average EMG within the window period based upon the corresponding subtracted response. This process was repeated for all phases of the cycle. The gain of

the reflex as a function of the phase in the movement cycle was thus obtained. The responses occurring at various phases of the cycle were also plotted against the mean level of background EMG activity in each of the phases.

CHAPTER 3

MOTOR CO-ORDINATION OF HUMAN HAND MUSCLES DURING RHYTHMIC FINGER MOVEMENTS AND HANDWRITING

3.1 Introduction

It has been mentioned in Chapter 1: General Introduction that many rhythmic behaviours, like ventilation, chewing and locomotion are widely accepted to be generated by networks of sets of interconnected neurones within the *CNS* which form a *CPG*. Rhythmic behaviours, such as various forms of locomotion, walking, running, stepping, flying and swimming, etc., have been extensively studied in both invertebrate and vertebrate species over the last century (Grillner, 1975, 1979; Andersson *et al.* 1981; Grillner *et al.* 1995). Manipulative finger tasks, for instance handwriting, typing and the like, are another form of rhythmic motor acts involving a central motor ‘program’ which is highly dependent on learning.

The motor contribution of the cerebellum was first recognised by Flourens in 1824. He suggested that the function of the cerebellum is to co-ordinate movement. Motor system research has revealed that the cerebellum participates in several aspects of motor behaviour. The valuable findings of Chambers & Sprague (1951) together with neurological studies in cerebellar patients (Holmes, 1917) established that the action of the cerebellum in different classes of motor functions may be mediated by different regions of the cerebellum. This inference was drawn on the basis of the fact that lesions in different cerebellar regions produced consistently different motor abnormalities. Both animal and clinical data indicated that midline lesions of the cerebellum primarily affected postural stability and gait, whereas more lateral lesions involving the cerebellar hemispheres caused abnormalities in the co-ordination of volitional movements. Several experiments within previous years have suggested that the cerebellum plays an important role in co-ordination control of the movements during visuo-motor tracking movements. Vercher and Gauthier (1988) examined the effects of dentate lesions on the co-ordination of the eye and hand motor systems during the ocular-manual tracking tasks in baboons. Their experimental results indicated that the cerebellum is involved in the co-ordination control of two separate systems. Cody, Lövgreen and Schady (1993) studied the dependence of movement performance upon visual information during

visuo-motor tracking in cerebellar patients. They concluded that the intact cerebellum participates in the proprioceptive guidance of voluntary movements. It is evident that, within each system, subco-ordination of different muscles and joints involved in the control of the movement is essentially required for achieving the desired movement.

Recent human physiological studies reflect the increased emphasis in upper limb and hand movement. Most studies in hand motor control have focused on specific aspects of muscle performance, either in essentially steady state conditions or isolated finger movements rather than the co-ordinated, rhythmic actions of combinations of different muscles required in performing such tasks as handwriting. Isolated finger movements have been investigated previously under the performance of finger flexion, extension, abduction or opposition, particularly thumb, index finger and middle finger (Long & Brown, 1964; Lawrence & De Luca, 1983; Darling & Cole, 1990; Bremner, Baker & Stephens, 1991). In addition, more advanced hand functions, such as reaching, grasp, power grip, precision grip, finger manipulations, have been paid much attention on the basis of combining electromyographic and kinesiological methods (Buchholz & Armstrong, 1992; Edin, Westling & Johansson, 1992; Jeannerod, 1994). Studies concerned with mechanisms of co-ordination were centred on individual fingers under static conditions (Cole & Abbs, 1986; Darling, Cole & Miller, 1994) or forearm movement in non-repetitive mode (De Luca & Mambrito, 1987; Paulignan *et al.* 1989; Sergio & Ostry, 1994). On the other hand, muscle performance involving constant isometric voluntary contraction has been the focus of investigating muscle fatiguability over previous years (Bigland-Ritchie *et al.* 1983; Enoka, Robinson & Kossev, 1989). Furthermore, the use of computerised techniques in motion analysis, together with neurophysiological methods, have made it possible to describe the pattern of more complicated cyclical hand movements and to identify the central mechanisms of the CNS involved in the control of these movements.

Manipulative tasks, such as writing, which combine several different types of simple movements, are performed with fine motor skills. Writing comprises a

comprehensive array of rhythmical activities which require different muscles and joints working in a well-coordinated pattern and acting upon an effectively equilibrated system. Nearly all the intrinsic and extrinsic hand and forearm muscles are involved in producing precisely controlled biomechanical forces essential for writing. During the performance of handwriting, the five digits require the integration of no less than thirty-six muscles (Williams *et al.* 1989). Most hand and forearm muscles are variably activated. Agonist and antagonist muscles are activated alternately. Thumb and digit joints move from one position to another in order to adapt proper movements. Muscles around joints operate in correct balance of contraction. The motor system is designed to co-ordinate muscle activation through control of motoneuronal activity. Centrally programmed commands and peripheral feedback commands must be co-ordinated to produce movements such as flexion, extension, or abduction alone due to reciprocal activation, or muscle co-activation without movement. In order to achieve the finely controlled and co-ordinated muscular activity for efficient handwriting, sensory feedback from proprioceptors in the intrinsic and extrinsic muscles and joints must be accurately integrated into a centrally programmed, learned pattern of co-ordinated motor activity to generate a rhythmical alternation. Proprioceptive reflexes need to be modulated in gain to adapt them dynamically to the phase of the movement.

Therefore, the question arises as addressed: can we define any characteristic pattern of motor co-ordination of different hand muscles during the performance of a range of rhythmic manipulatory tasks representing different components of handwriting?

A preliminary report of part of this work has been presented at the Physiological Society Meeting (Xia & Bush, 1995).

3.2 Experimental protocol

Experiment I

Nineteen healthy volunteers (13 males and 6 females) and two writer's cramp subjects (2 males) attended this experiment which was aiming to investigate motor co-ordination patterns of different hand muscles during the performance of a range of rhythmic manipulative tasks representing different components of handwriting, discrete writing and ordinary writing tasks (Xia & Bush, 1995). Fifteen subjects, including two subjects with writer's cramp, were right-handed dominant and six left-handed dominant. Four muscles FPB, EPB, APB and 1DI of the dominant hand were studied in this series of experiments.

Each subject sat on a height-adjustable chair with his dominant hand on the table. They were trained to perform a standard protocol comprising several distinct rhythmic manoeuvres, for 10-15 cycles each following an auditory cue set at 1 Hz frequency, with a short period rest between tasks:

- (1) *Thumb flexion/extension (FE)*: the subject, with forearm supinated and hand flat on the table, performed thumb flexion and extension repetitively.
- (2) *Abduction/adduction (AB)*: with forearm pronated and hand flat on the table, thumb adducted and index finger abducted simultaneously until they closed together, then thumb abducted and index finger adducted rhythmically.
- (3) *Vertical writing in stencil (VW)*: subjects held a pen to draw a 12.5 mm line up and down in the 'Y-axis' direction, the pen-tip movements being monitored by means of a linear slide potentiometer.
- (4) *Horizontal writing in stencil (HW)*: subjects held a pen to draw a 12.5 mm line in the 'X-axis' direction, the pen-tip movements being monitored in the same way.

Before the recording sessions began, the isometric maximal voluntary contraction (MVC) was measured separately for each recorded muscle against resistance. The MVCs were defined as the average of three reproducible measurements.

Movements performed in this experiment, including various repetitive finger manipulations and discrete elements of writing, were selected because they are involved in normal handwriting. EMG signals from one normal right-handed and one left-handed subject were not successfully recorded, so data recorded from these two subjects were excluded. Results obtained from writer's cramp subjects will be discussed in Chapter 6.

3.3 Results

Muscle activity patterns during repetitive finger movements and component writing

Examples of raw EMG recordings from four muscles during part of a series of repetitive finger movements and a short segment of component writing are shown in Figure 3.1 for one right-handed subject. Figure 3.1A clearly illustrates rhythmical EMG activities simultaneously recorded from four hand muscles during six cycles of thumb flexion and extension. The EMG bursts were alternately seen in thumb flexor FPB and extensor EPB, which are a pair of agonist and antagonist muscles. Muscles APB and 1DI were synchronously activated with muscle FPB. Figure 3.1B demonstrates the EMG activity patterns from the same four muscles for the same subject while drawing a vertical line repetitively with his normal pen-grip. The muscular activity during a component writing task apparently shows a more static pattern than that during ‘thumb flexion/extension’ task. This muscle activity pattern was observed in all subjects. Generally, the EMG activity during relatively isolated finger movements shows more rhythmic, dynamic motor pattern than during highly skilled writing task which normally requires several muscles working in a well-coordinated way.

Task-related co-ordination patterns during rhythmic hand movements

Modulation of EMG amplitude from the same four muscles during four different tasks is shown in Figure 3.2 in the format of phase diagrams (Xia & Bush, 1996b). EMG activity was averaged over approximately 10 individual cycles of each movement for each subject. The phase diagrams illustrated in Figure 3.2 were each averaged across 12 right-handed subjects. EMG activities recorded from muscles for one subject were not included in the average because of the poor contact between electrodes and skin. Both cycle period and EMG amplitude were normalised, the latter to the maximum of the means.

During rhythmic activity, flexion and extension of thumb or fingers usually appear at different phases alternately to maintain the cyclical movement. While performing the task ‘thumb flexion/extension’, FPB acted as an agonist muscle and EPB as an antagonist for flexion phase, and vice versa for extension phase (Figure 3.2A). The onset time of each cycle was recognised as the starting point of the FPB burst. EMG amplitude was strongly modulated in all muscles for this task. Muscles FPB and EPB were alternately activated. APB and 1DI show synchronous activity with FPB. When subjects performed the ‘abduction/adduction’ task, the thumb and index finger adducted and abducted rhythmically. All four muscles activated in a highly modulated way (Figure 3.2B). The starting time of each cycle for this movement was based on 1DI muscle activity. The primary agonists for this task are 1DI and APB which were active through the abduction phase. 1DI and EPB presented monophasic activity patterns. FPB and APB showed biphasic patterns. The activation patterns of 1DI, APB and FPB were consistently observed in all subjects during this task. EPB was relatively variable across the subjects.

The ‘vertical writing’ and ‘horizontal writing’ tasks studied here belong to discrete movements of handwriting which are directly related to normal cursive handwriting. In comparison with the ‘thumb flexion/extension’ and ‘abduction/adduction’ tasks, the degree of EMG amplitude modulation of all four muscles during vertical and horizontal writing was much lower (Figure 3.2C, D). Motor output patterns from these muscles during vertical and horizontal writing were characterised by a static and tonic pattern. It is noteworthy that the 1DI muscle presented similar activity pattern to FPB muscle particularly during the tasks ‘thumb flexion/extension’, ‘vertical writing’ and ‘horizontal writing’. The correlation coefficients between 1DI and FPB are 0.808, 0.673 and 0.825 for these three tasks, respectively.

It is clearly illustrated in Figure 3.2 that EMG amplitudes of four muscles were much more strongly modulated during tasks ‘thumb flexion/extension’ and

‘abduction/adduction’ than during ‘vertical writing’ and ‘horizontal writing’. Here, EMG peak to peak amplitude was used to quantitatively express the depth of modulation for each muscle. EMG activity was averaged over 10-15 movement cycles for each subject. Due to the large variation of EMG activity level between subjects, EMG amplitudes were normalised to the maximum within the averaged movement cycle. Normalised peak to peak amplitudes were averaged across 12 right-handed subjects during each task for each muscle, and are shown as mean + s.e.m. in Figure 3.3B. Statistical analysis of these data using Student *t*-test indicated that there were no significant differences between tasks ‘thumb flexion/extension’ and ‘abduction/adduction’, and between tasks ‘vertical writing’ and ‘horizontal writing’ for all four muscles. However, the depth of modulation was significantly greater during tasks ‘thumb flexion/extension’ and ‘abduction/adduction’ than during ‘vertical writing’ and ‘horizontal writing’, in the right-handed subjects. In particular, 1DI amplitude modulation during ‘abduction/adduction’ was much stronger than that during vertical and horizontal writing (two-tailed $p < 0.0001$). Comparisons of the depth of amplitude modulation between four tasks for each muscle in 12 right-handed subjects are given in Table 3.1.

Relation of movement patterns between right and left-handed subjects

The same format of display as Figure 3.2 for right-handed subjects is shown in Figure 3.4 for the left-handed group. The basic muscle activity patterns showed many similarities between these two groups. The cross correlation was investigated between right- and left-handed subjects during the same task for the same muscle. The product-moment correlation coefficients are given in Table 3.2.

The relationships between the two groups are, in most cases, highly correlated from each muscle during all tasks, except muscle EPB during ‘abduction/adduction’ and ‘thumb flexion/extension’, and 1DI during ‘horizontal writing’. The depth of amplitude modulation was compared between different handed subjects. The normalised amplitude modulation for 5 left-handers is shown in Figure 3.3A, in comparison with right-handers

Table 3.1. Comparisons of the depth of amplitude modulation between four tasks in 12 right-handed subjects. Two-tailed *p* values of student *t*-test between each of 4 tasks: thumb flexion/extension (FE), abduction/adduction (AB), vertical writing (VW) and horizontal writing (HW) for 4 muscles FPB, EPB, APB and 1DI. The depth of modulation shows significant differences between simple finger actions FE, AB and component writing tasks VW, HW. Those marked star (*) represent statistically significant at level of 0.0083 after Bonferroni procedures was applied.

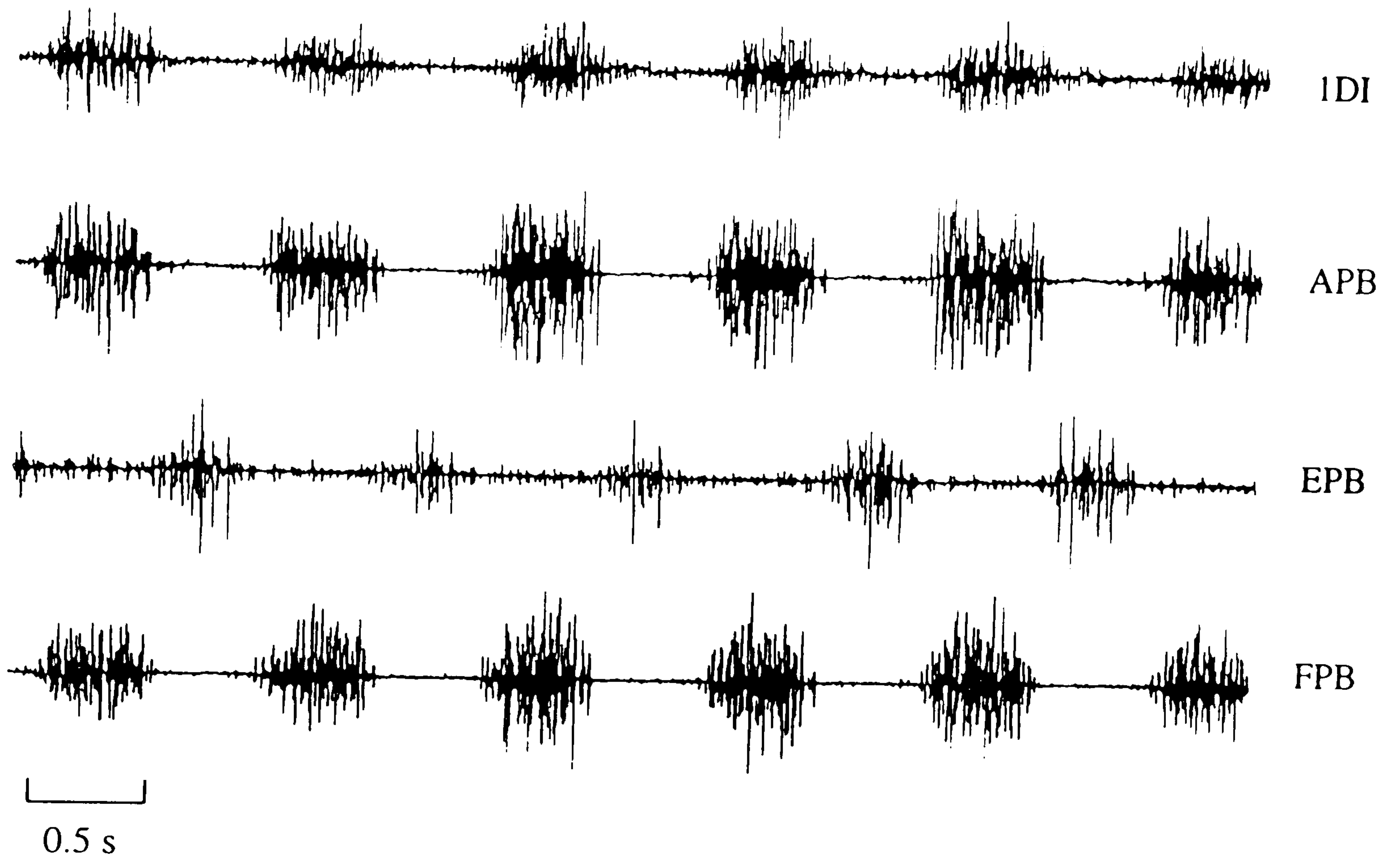
FPB						EPB					
n		FE	AB	VW	HW	n		FE	AB	VW	HW
12	FE		0.235 n.s.	0.002*	0.0001*	12	FE		0.5803 n.s.	0.012 n.s.	0.137 n.s.
12	AB			0.022 n.s.	0.002*	12	AB			0.057 n.s.	0.370 n.s.
12	VW				0.283 n.s.	12	VW				0.276 n.s.
12	HW					12	HW				
APB						1DI					
n		FE	AB	VW	HW	n		FE	AB	VW	HW
12	FE		0.130 n.s.	0.019 n.s.	0.0003*	12	FE		0.013 n.s.	0.001*	0.001*
12	AB			0.068 n.s.	0.014 n.s.	12	AB			<0.0001*	<0.0001*
12	VW				0.418 n.s.	12	VW				0.660 n.s.
12	HW					12	HW				

Table 3.2. Correlation coefficients between mean values of EMG amplitude in 12 right-handed and 5 left-handed subjects.

Muscle\Task	<i>FE</i>	<i>AB</i>	<i>VW</i>	<i>HW</i>
<i>1DI</i>	0.698	0.983	0.865	0.232
<i>APB</i>	0.909	0.738	0.759	0.757
<i>EPB</i>	0.418	-0.067	0.632	0.756
<i>FPB</i>	0.929	0.688	0.618	0.747

whose data are shown in Figure 3.3B. Statistical analysis using student *t*-test confirmed that the differences in amplitude modulation between left and right-handers were not statistically significant for any muscle during any of the tasks, except in one case in which 1DI modulation of the right-handed group was significantly greater than that of the left-handed group during ‘thumb flexion/extension’. These statistical analyses suggested that there was a similar modulation pattern of each muscle during specific tasks between right- and left-handed groups.

A



B



Figure 3.1. Raw EMG recordings from muscles FPB, EPB, APB and 1DI for one subject during *A*: thumb flexion/extension; *B*: vertical writing.

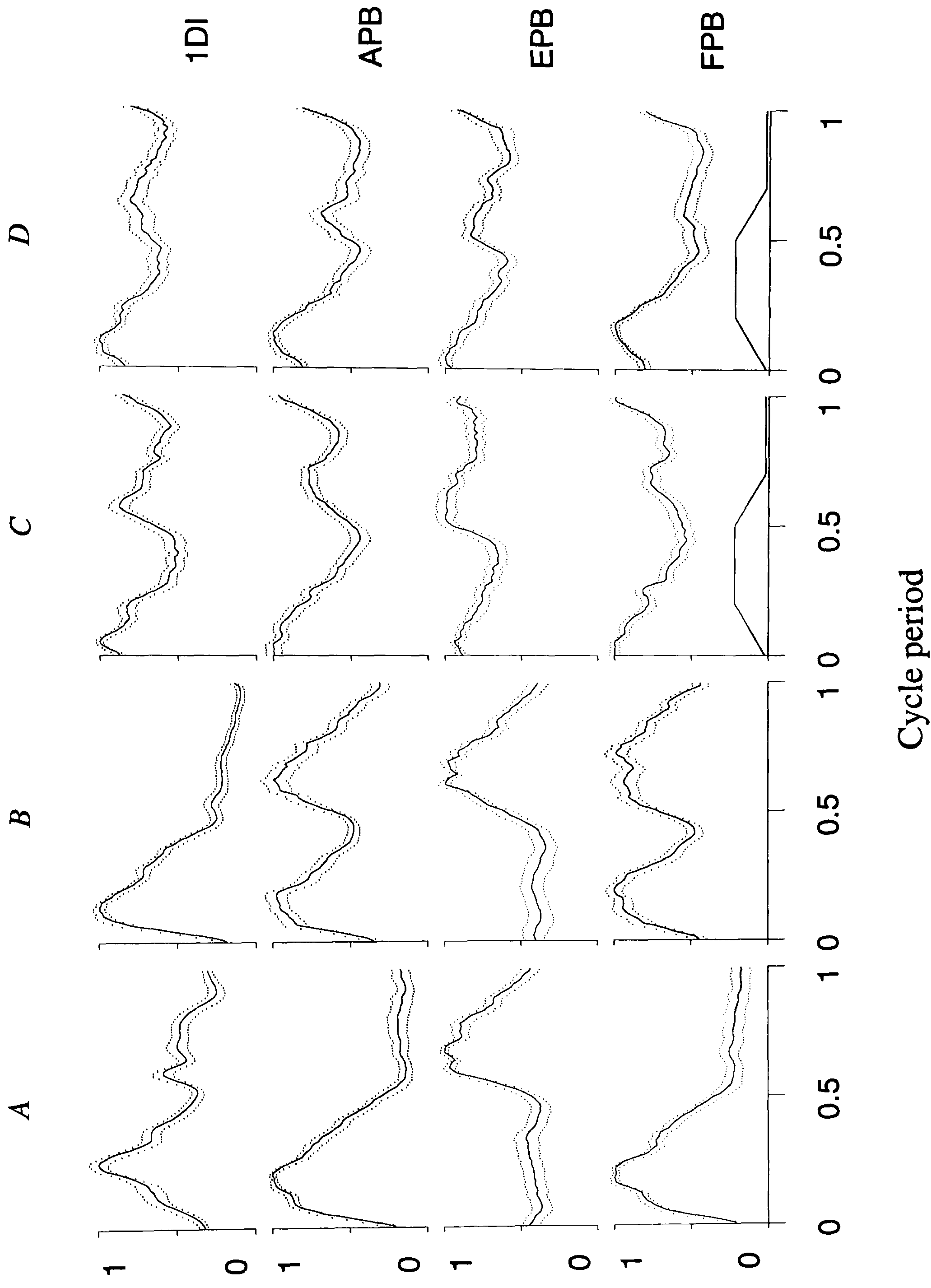
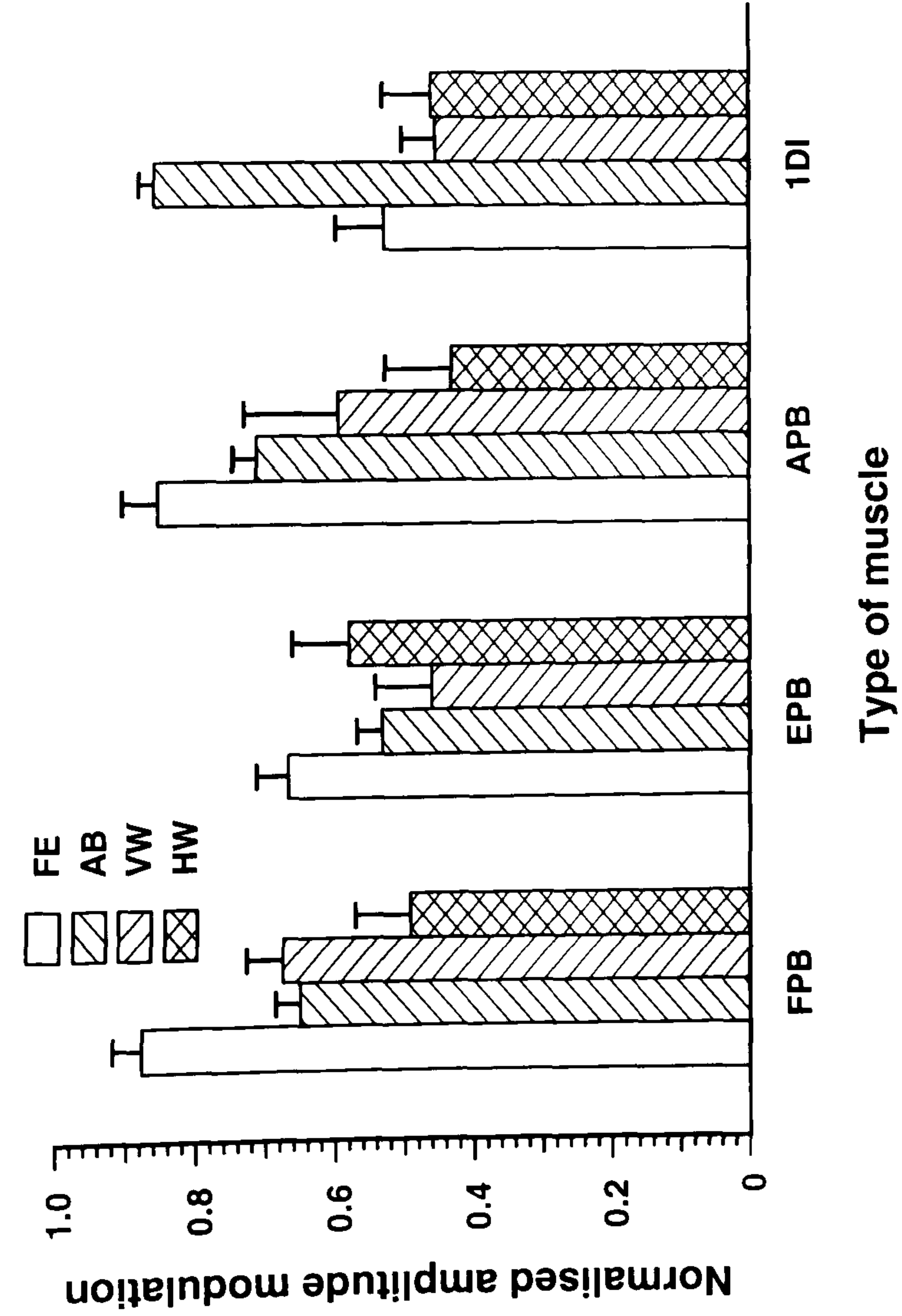


Figure 3.2. Phase diagrams of rectified, filtered EMGs from four muscles indicated above during 4 tasks averaged over 10 cycles in 12 right-handed subjects. *A*: thumb flexion & extension; *B*: abduction & adduction; *C*: vertical writing; *D*: horizontal writing. Ramp signals in *C* and *D* were recorded to monitor ‘vertical’ and ‘horizontal’ writing movements. **X**-axis: normalised cycle period (approximately 1 sec); **Y**-axis: normalised EMG amplitude; *Solid lines*: mean EMG activity; *Dotted lines*: s.e.m.

A



B

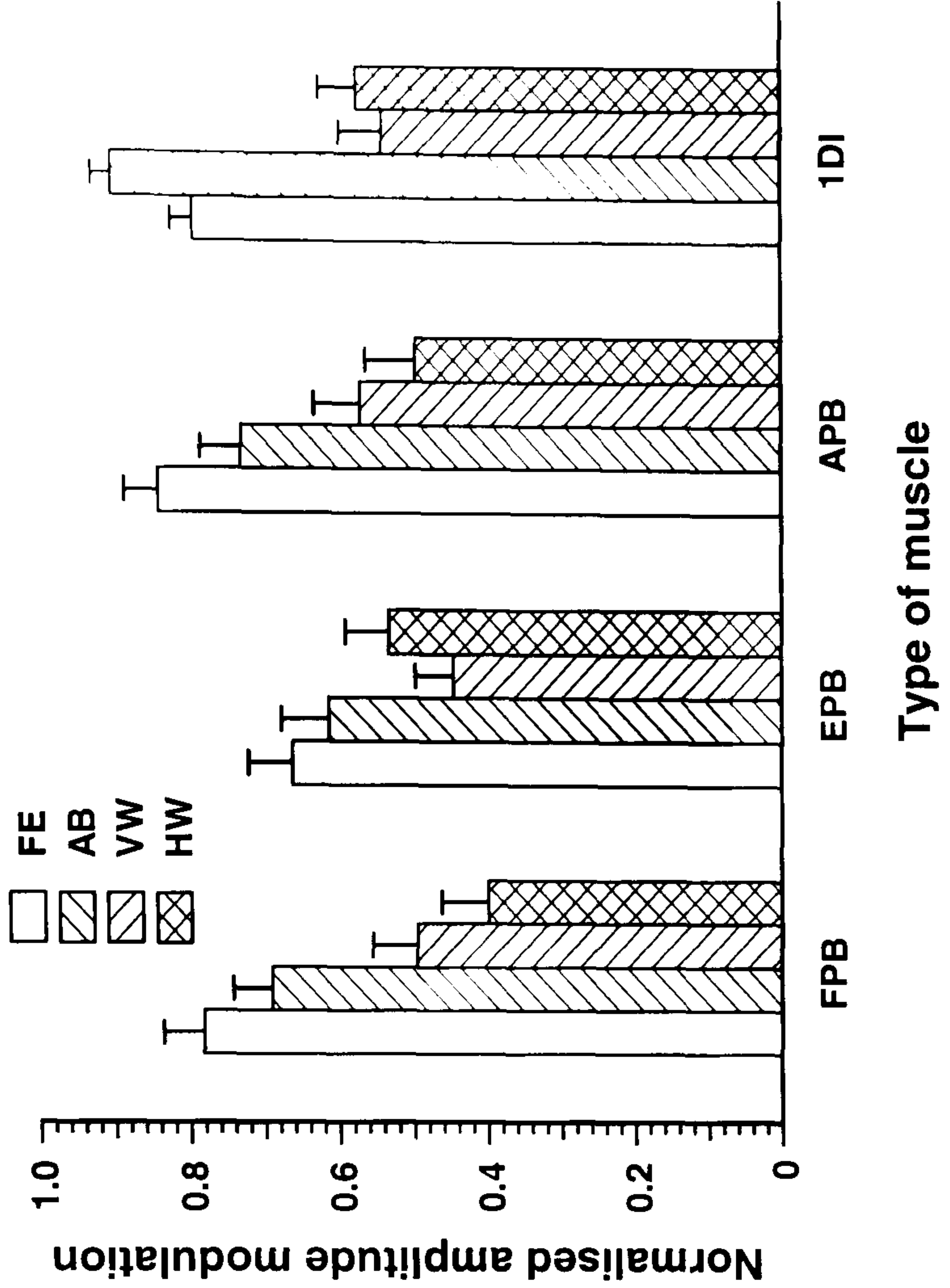


Figure 3.3. Normalised amplitude modulation of four muscles during 4 different tasks as indicated: FE (thumb flexion/extension), AB (thumb & index finger abduction/adduction), VW (vertical writing) and HW (horizontal writing). Each bar represents the mean + s.e.m. *A*: 5 left-handed subjects; *B*: 12 right-handed subjects.

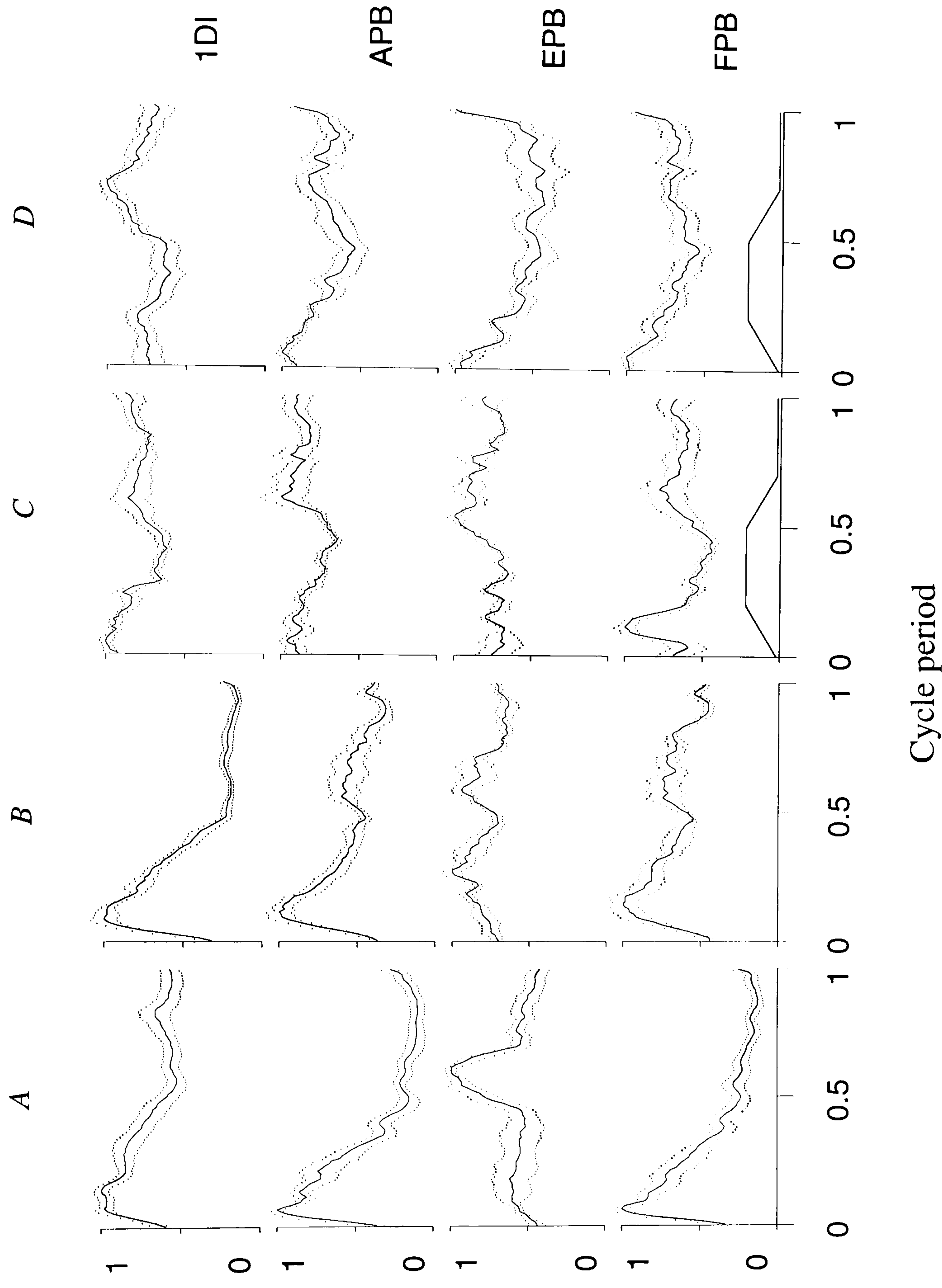


Figure 3.4. Phase diagrams of rectified, filtered EMGs from four muscles indicated above during 4 tasks averaged over 10 cycles in 5 left-handed subjects. *A*: thumb flexion & extension; *B*: abduction & adduction; *C*: vertical writing; *D*: horizontal writing. Ramp signals in *C* and *D* were recorded to monitor ‘vertical’ and ‘horizontal’ writing movements. **X**-axis: normalised cycle period (approximately 1 sec); **Y**-axis: normalised EMG amplitude; *Solid lines*: mean EMG activity; *Dotted lines*: s.e.m.

3.4 Discussion

Due to the complexity of handwriting movement, we have selected a variety of simple isolated rhythmic finger movements and component writing tasks which represent typical handwriting. As mentioned earlier, normal cursive handwriting is composed of vertical, horizontal, oblique lines and some loops equivalent to circular and oval shapes. Muscles selected for this protocol are all closely involved in writing. FPB, EPB and APB act as thumb flexor, extensor and abductor. 1DI acts to abduct the index finger as well as to have strong rotatory action at the metacarpophalangeal joint. 1DI, involved in very fine manipulatory skills, has been the most extensively studied muscle for investigation of hand motor control. Analyses of hand muscle activity during these actions reflect the muscular motor co-ordination while performing repetitive finger actions including handwriting.

As is well known, rhythmic behaviours are controlled by the *CPGs* (Grillner, 1975, 1979) within the neural circuitry of the spinal cord, essential for locomotion as well, which has been extensively studied for over a century. The pattern generators for rhythmic activities are regarded as biological oscillators. Many biological oscillators operate on the basis of reciprocal inhibition of circuits, called half-centres, that control antagonistic muscles. Excitation of an extensor muscle by one half-centre is accompanied by reciprocal inhibition of the half-centre for the antagonistic flexor muscle. When the excitation of the extensor muscle decreases, there is less inhibition of the antagonist, which can then be activated by the second half-centre. This results in reciprocal inhibition of the first half-centre. The details of this mechanism and factors causing switching between the two half-centres vary with each particular oscillator being considered (Brown, 1914; Grillner, 1975; Berne & Levy, 1993). These mechanisms apply not only in locomotion, but also in various other rhythmic motor acts, possibly including repetitive hand movements. The importance of reciprocal inhibition has also been recognised in hand muscles. In normal conditions, agonist and antagonist muscles show alternating activation during rhythmic movements as an example from

this study is shown in Figure 3.2. During simple “thumb flexion/extension” task, thumb flexor and extensor were activated alternately (see Figure 3.2). Both muscles function as a pair of agonist and antagonist muscles for this particular action. Joint motion is based upon one muscle activated and the other deactivated. As the thumb approaches its furthest position, sensory signals may promote the switch from flexion to extension and vice versa, as well as the feedback involved in the movement. Similar rhythmic pattern has been seen in leg muscles in locomotory system (Andersson *et al.* 1981; Grillner *et al.* 1995). During finger ‘abduction/adduction’ movement, the primary agonists for thumb and index finger abduction are APB and 1DI which were active through their individual abduction phases. Identification of the onset time of each cycle for this movement was based on 1DI muscle. 1DI and EPB presented monophasic activity patterns and the burst appeared at different phases. FPB and APB showed biphasic patterns in this task.

However, reciprocal inhibition is not the only possible organisation of a motor control system. In some cases, motor commands will produce co-contraction of synergists and antagonists. For example, when a person makes a fist, this happens. The muscles that extend and flex the wrist contract and allow the wrist to resist motion (Berne & Levy, 1993). An example obtained from this study is demonstrated in Figure 3.2 as well. ‘Vertical writing’ and ‘horizontal writing’ belong to component writing which is directly involved in normal handwriting. Finger flexion and extension are involved in the performance of the task ‘vertical writing’, whereas finger abduction and adduction are involved in ‘horizontal writing’. In comparison with the tasks ‘flexion/extension’ and ‘abduction/adduction’, EMG patterns of all the muscles for the tasks ‘vertical writing’ and ‘horizontal writing’ are characterised by a relatively tonic pattern. The observation can be explained as due possibly to the following reasons. These two movements were performed by following a slide potentiometer which was confined into the limited length 12.5 mm, and proprioceptive feedback system regulates and controls the motor tasks more subtly during delicate, precision manoeuvres than those relatively simple isolated movements. Each muscle shows comparable activity

patterns in both tasks. There is a slight phase shift between 'vertical' and 'horizontal' writing tasks observed from both FPB and APB. Within the same task, a certain amount of co-activation is required to maintain the joint stable in order to hold the pen steadily.

Intrinsic muscles have been considered to be of importance in performing very fine, delicate manipulations involving a precision grip. EMG studies show that APB muscle strongly contracts in the activities of holding a pen, painting and playing a piano (Wynn-Parry, 1981). 1DI is involved in very fine, delicate finger manipulations. EMG phase analyses show that 1DI presents a similar pattern to FPB and APB during the tasks 'thumb flexion/extension', 'vertical writing' and 'horizontal writing'. This result implies that 1DI appears to play a distinctive synergistic role in a variety of manoeuvres involving the thumb and index finger. Muscles FPB and APB show a similar pattern, simultaneous activity mode, which is observable during all the manual tasks illustrated in Figure 3.2. There may be two reasons: (1) both muscles behave synergistically; and (2) cross talk recorded during movement, due to the close location in the thenar region of the hand. To avoid cross talk, needle electrodes could be used in this situation instead of surface electrodes.

From the present results, no obvious difference was observed between right-handed and left-handed groups. Some left-handers flex the wrist, called hooked writing posture, when they perform writing tasks. Left-handed subjects who participated in our experiments, do not use the hooked writing posture. And the muscles selected under study are mostly intrinsic muscles, except for the extensor pollicis brevis. Muscle activity patterns may appear to be different if the hand or wrist display different postures. Long and Brown reported in 1964 that the electromyographic activity of the flexor digitorum superficialis varies with wrist position, being least in the extended and greatest in the flexed attitude. Therefore, either writing posture or the muscles being studied may contribute to the muscle activity patterns. The high correlation of muscle activity patterns between right and left-handed subjects implies that motor commands

sent to the dominant hand, irrespective of right or left-handed, are primarily similar during the tasks investigated here.

In this chapter, we have shown how different hand muscles work co-ordinately together as a unit in order to acquire smooth, efficient writing. In this experiment, component writing was performed with the aid of stencils. The same form of movements by freehand have been included under a separate protocol in which the patterns of muscle activity will be examined in a broad range of both right and left-handed subjects, including ones who employ the various common or abnormal pen-grips. This part of the study will be discussed in the following chapter.

CHAPTER 4

HAND MUSCLE EMG PATTERNS DURING REPETITIVE ‘WRITING’ TASKS IN PEOPLE WITH DIFFERENT PEN GRIPS

4.1 Introduction

It has been described in Chapter 3 that handwriting, performed with very fine motor skills, also involves rhythmic activity which requires different muscles and joints working in good co-ordination and concert. As described in Chapter 1 and illustrated in Figure 1.3, ten types of operational pen-grip have been given on the basis of a literature review (Schneck & Henderson, 1990; Schneck, 1991). Here, the muscle activity patterns of a few relatively mature pen-grips were studied during writing. Most adults holding a writing implement use what has been termed by Wynn-Parry (1966) as the dynamic tripod grip (DTG). The standard DTG is a finger posture having the writing tool resting on the distal aspect of the middle finger while being controlled between the pads of thumb and index finger. The dynamic tripod grasp is generally considered as the most desirable grasp pattern for control of the pen or pencil (Weiser, 1986) and is widely believed to be the most efficient grasp for writing. In the developmental literature, the DTG grasp is described as the most mature grasp pattern and therefore is the targeted pencil grasp among educators and therapists, acquired between the ages of 4 and 6 years (Rosenbloom & Horton, 1971; Saida & Myashita, 1979; Erhardt, 1982; Schneck & Henderson, 1990).

Although the DTG grasp is the most common way of holding a pen in normal handwriting, a variety of alternative grips are seen, even in adults, including the lateral tripod grasp, multiple finger grasps, e.g. the similar four finger grasp or “dynamic quadripod grip” and a rare “five finger grasp” and other even less commonly used grips (Alston & Taylor, 1987; Bergmann, 1990). Several investigators have reported the incidence of atypical pencil or pen grasps among non-dysfunctional adults and children which challenged the traditionally accepted need for the DTG grip (Jaffe, 1987; Bergmann, 1990; Schneck & Henderson, 1990). Results reported by Bergmann documented that 85.7% of the total 447 right-handed subjects used the dynamic tripod grip, 10.1% of the sample used the lateral tripod grip, less than 2% of the total sample used a variety of non-tripod grasps for their daily writing needs. Schneck and Henderson

(1990) found that 25% of the 6 year-old non-dysfunctional children demonstrated a lateral tripod grasp on a pencil. Jaffe (1987) investigated the effect of grip on writing speed, legibility and long-term endurance in adult handwriting. It was found that there were no significant differences between the typical dynamic tripod grasp and other atypical grasps, including the lateral tripod grasp and multiple finger grasps. This finding was supported by Ziviani and Elkins (1986) who reported that no statistical significance was shown among even the most abnormal patterns while considering the impact of different grasps on writing speed and legibility amongst a sample of 218 children attending regular schools. These studies suggested that the concept of proper pencil or pen grip be expanded to allow for more variations.

The presence of writer's cramp signifies a dysfunctional grip that is applying undue strain on specific muscle groups. Dystonic postures of the hand typically occur in writer's cramp while picking up a writing implement. The pen is commonly held very tightly, with an exaggeration of the normal posture of thumb, index and other fingers, and with hyperextension of the distal interphalangeal joints of the index finger (Sheehy & Marsden, 1982). A typical writer's cramp may present the common feature of elevation of the elbow, hyperpronation of the forearm. Many patients change the posture of holding the pen in an attempt to overcome difficulties with writing, sometimes holding it vertically between the index and middle fingers, or in a closed fist. Some patients hold the pen with the thumb, middle, ring and little fingers flexed across the palm. Some lift the index finger off the pen and extend it. Some hold the pen between thumb and lateral side of the index finger and twist the hand excessively (Sheehy, Rothwell & Marsden, 1988).

Previous studies have pointed out that there is no direct correlation between postures of pen holding and writing speed, legibility and fatigue. It has been suggested by Keogh and Sugden (1985) and Boehme (1988) that the ability to form letters has less to do with the prehension pattern used and more with the extent to which the grasp allows for use of the intrinsic hand musculature, smooth co-ordination of movements

and precision control. We have studied the co-ordination of different hand muscles during rhythmic finger movements related to writing, as described in Chapter 3. EMG activity patterns may reflect the muscle co-ordination strategies adopted in different ways of holding the writing implements. Some of the less common grips might represent strategies to overcome difficulties in controlling the pen with the typical DTG. Therefore, the purpose of this study is to investigate whether the style of pen grip influences the modulation patterns of hand muscle activity during various forms of handwriting. Pen-grips employed in this study included the dynamic tripod grip using three fingers, four finger grasp (4FG) using four, and five finger grasp (5FG) using five.

4.2 Experimental protocol

Experiment II

This experiment was designed to compare the patterns of muscle activity produced by individuals who use the standard dynamic tripod (DTG) grip, and others employing unusual pen grips, e.g. four finger grasp (4FG) and five finger grasp (5FG). Experiments were performed in both right and left-handed subjects during repetitive writing tasks (Xia & Bush, 1996a). A total number of 23 healthy subjects (12 males and 11 females) voluntarily took part in this test, including nine right-handed and five left-handed with the standard DTG, six right-handed and one left-handed using 4FG, one right-handed and one left-handed with 5FG grips. Pairs of self-adhesive surface electrodes were used to record EMG signals simultaneously from two intrinsic hand muscles: flexor pollicis brevis and 1st dorsal interosseous, and two extrinsic forearm muscles: flexor digitorum superficialis and extensor digitorum communis.

Each subject sat comfortably with his dominant hand on a table to perform a range of simple manipulative tasks involving finger movements related to handwriting, following an audible click pulse to repeat rhythmically at 1 Hz for 10-15 cycles. Subjects were given some preliminary trials to practise each task before the recordings were made. These tasks included:

- (1) *pen-grip*: each subject held a pen with his usual pen-grip to press down and then to relax repetitively at 1 Hz, with the one-way force pen-tip on a cantilever brass beam and the index finger pressing on the force pen beam.
- (2) *opposition*: each subject was asked to perform rhythmic isometric opposition with a pen between thumb and index finger, repetitively squeezing the pen isometrically, with the index finger pressing on the force pen beam.
- (3) *Horizontal writing (HW)*: each subject held a pen to draw a 12.5 mm line in the 'X-axis' direction, either on a slide potentiometer or by freehand.

(4) *Oval writing (OW)*: subjects drew an oval using a stencil and again by freehand in clockwise and anticlockwise directions and with the oval sloping to the right and left at 45 degrees.

(5) *Word writing*: each subject was asked to write a non-sensical word “smegbred” in lowercase repetitively, 10 times by freehand only.

During freehand writing, the pen-tip was connected to a closed circuit in order to monitor the movement. Subjects were asked to draw horizontal lines back-and-forth, or an oval shape crossing the edge of the foil during tasks ‘horizontal writing’ and ‘oval writing’, and to write words on the foil during the task ‘word writing’. During stencil writing, a very fine wire was fixed on the top of the oval where the pen-tip would make contact during task ‘oval writing’. A pulse was produced when the pen-tip made contact with the foil or the wire on the stencil. The signals were recorded along with the EMG signals during the performance of the tasks as an indicator of each cyclical movement.

4.3 Results

A total number of 23 subjects were divided into 6 groups: 9 right-handed and 5 left-handed subjects with the standard DTG grasp, 6 right-handed and 1 left-handed subjects using the 4FG, 1 right-hander and 1 left-hander with the 5FG grip. In three of these groups, there was therefore only one subject reflecting the fact that these grips were rather uncommon. Consequently, some of the results shown in this part were mainly summarised from the relatively larger sampled groups.

Hand muscle EMG activity patterns during writing

Figure 4.1 shows recordings from four hand muscles and two monitor signals from one right-handed subject with the standard DTG grip while writing a non-sensical word “smegbred” repetitively by following a metronome set at 0.2 Hz. Most subjects could complete writing the word “smegbred” within 4 s. EMG activity was simultaneously recorded from muscles FPB, 1DI, FDS and EDC, as shown in traces 3-6. The second trace displays the force signal resulting from the pressure which the index finger exerted on the force pen during writing. The top trace shows the period when the pen-tip made contact with the aluminium foil during each word (pulse) and this corresponded with the timing of the EMG burst. The force pen monitor also illustrates increased index finger pressure on the pen during the pen-tip contact periods.

EMG phase diagrams were constructed by averaging EMG signals over 10 cycles normalised with respect to phase and amplitude. Examples of EMG phase diagrams from 1 right-hander (KF) with the DTG and 1 right-hander (MD) with the 4FG are shown in Figure 4.2 for writing “smegbred”. The X co-ordinate has been normalised in relation to the cycle period, which is the period of the pen-tip contact in this case. The Y co-ordinate shows the normalised amplitude relative to the maximum. EMG rhythmicity was clearly observed in all the muscles recorded while writing both word and individual letters. This kind of EMG activity pattern was seen in all the subjects participating in the experiment. The observation described here confirmed that writing

involves rhythmic activity. Alternate activation existed between finger flexor (FDS) and extensor (EDC) in both subjects, confirmed by the negative correlation between these two muscles. In contrast, muscle activity showed co-activation pattern between FPB and 1DI, indicated by positive correlation between those two. This is in agreement with the observation reported in Chapter 3 that 1DI appears to play a synergistic role with FPB in a variety of finger manoeuvres.

Correlation between tasks ‘pen-grip’ and ‘opposition’

Opposition of the thumb and index finger plays an important role in very fine finger manipulations. Whether there is any correlated relationship between opposition and posture of pen-holding is interesting to investigate. Each subject was asked to perform two rhythmic tasks in this experiment: (1) holding a pen with their usual pen-grip, to press repetitively at 1 Hz with the pen-tip on a cantilever brass beam; (2) repetitive opposition of thumb and index finger at 1 Hz, with the forefinger pressing on the one-side force pen beam. Figure 4.3 shows EMG phase diagrams of four muscles while performing these two tasks averaged over 10 movement cycles in one left-handed subject with the DTG grip. The starting point of the cycle was identified as half-amplitude on rising phase of the force in this instance. The primary activity pattern of each muscle seems to be fairly similar between the two tasks. EMG amplitude during the two tasks was plotted against each other for each of the four muscles, as illustrated in Figure 4.4. Cross-correlation coefficients, which are given in the figure legend, were computed between the two tasks for each muscle in this example. Results indicated that EMG amplitude was highly correlated between the two repetitive movements for all the muscles. This result suggested that opposition of the thumb and index finger is of functional importance during writing with the DTG pen-grip.

Modulation patterns of hand muscles in different pen-grips during component writing

Normal cursive handwriting is considered to comprise loops, such as circle, oval and lines with different orientations, e.g. vertical, horizontal or oblique lines drawn on a

planar surface. As described in the Experimental protocol, each subject performed several line and loop drawing tasks repetitively either by tracing a stencil or freehand. Generally, each task was performed for 10-15 repetitions. EMG activity was averaged by phase between individual cycles for each subject within the same group.

EMG was averaged over a number of subjects for each pen-grip during oval drawing by both stencil and freehand. The number of subjects was 9, 5 and 1 for pen-grips DTG, 4FG and 5FG in right-handers, respectively. The EMG average from individual subjects was obtained by averaging 10 successive oval drawings. Figure 4.5 shows phase diagrams of four muscles during repetitive clockwise drawing of an oval shape (1.2 cm long axis sloping at 45° to right) in stencil (S) and freehand (F). The standard error of the mean of the data is presented in Figure 4.5. Phase diagrams illustrate that the extent of amplitude modulation was much smaller in DTG and 4FG grasps than in 5FG grasp. There was little difference in modulation patterns between stencil and freehand drawings for each muscle in each grip.

The depth of modulation was measured as peak to peak rectified EMG amplitude, which was normalised with respect to the maximal value. Pooled data were plotted in Figure 4.6 in order to compare between different pen-grips during stencil drawing. The 5FG group included only one subject in whom the EMG amplitude of the four muscles was strongly modulated. Student *t*-test was used to compare the DTG and 4FG grasps and these indicated that the difference in the depth of amplitude modulation was not statistically significant for each muscle studied ($p>0.05$). A comparison of amplitude modulation between stencil and freehand drawing for each grip and each muscle, is shown in Figure 4.7 (mean \pm s.e.m. across subjects with the same grip). Freehand drawing was compared with stencil drawing for each muscle in DTG and 4FG grips separately. The paired *t* test results revealed that there was no statistically significant difference between stencil and freehand drawing for all four muscles in both DTG and 4FG groups. The depth of modulation in one subject with 5FG grip was greater than that in the other two groups. However, no statistical test could be performed

on this group which was represented by a single subject. In general, the statistical analysis on the data shown in Figure 4.6 and 4.7 is in agreement with the visual observation of the data. Similar modulation patterns were observed during anticlockwise drawing in stencil and freehand by the same group of subjects. Amplitude modulation was slightly greater in stencil than in freehand oval drawing. Phase diagrams of the left-handed subjects showed a similar pattern to that of the right-handed groups. Anticlockwise drawing in left-handers was comparable with clockwise drawing in right-handers, and vice-versa.

EMG activity patterns during stencil and freehand oval drawing have been illustrated in this section. What kind of modulation patterns can be observed in these muscles during stencil and freehand line drawing? Figure 4.8 shows examples of EMG phase diagrams in 5 right-handed subjects with the standard DTG grip during repetitive stencil and freehand horizontal line drawing. Each panel represents an average over 10 repetitions. Only the mean value of the data is presented in Figure 4.8. It should be noted that the EMG patterns during stencil writing has a 90° phase advance compared with those during freehand writing, since the phase of the movement was monitored in different ways (see Experimental protocol). The starting point of the cycle period was defined as the beginning to move the pen from left to right in stencil writing, and defined as the mid-point to move the pen from left to right in freehand writing. It is clear that, in most cases, amplitude modulation is greater in the constrained (stencil) than in freehand line drawing, suggesting a more refined influence of sensory feedback in regulating and controlling freehand writing actions.

Relation between EMG activity patterns and force during ‘pen-grip’ task

The relationship between EMG activity patterns and the force produced by the index finger was investigated in a right-handed group of subjects with the standard DTG. Subjects were asked to grip the force pen repetitively while the force exerted on the pen and the EMG activities from FPB, 1DI, FDS and EDC were recorded. Data from six of nine subjects in this group showed consistent muscle activity patterns during this

task. EMG activities from two subjects were completely tonic within the cycle period. Recording of force from another subject did not display force variation along the cyclical movement. Figure 4.9 illustrates averaged phase diagrams of EMG of all four muscles and force over 10 repetitions across 6 right-handed subjects with the DTG pen-grip, in whom the consistent muscle activity patterns were observed, during the repetitively gripping task. The standard deviation of the mean is not presented in the diagram because of the variable muscle activity levels between individual subjects. Phase diagrams show that EMG amplitudes of the intrinsic muscles are strongly modulated in this task, whereas the extrinsic muscles displayed constant, tonic activity patterns. In five of these six subjects, EMG of all four muscles reached the peak slightly phase advanced with respect to the force because of the contraction time of the muscle. The reversed pattern was observed in one subject. The averaged results show muscles FPB and EDC increased activity almost in parallel with the increase in force. Product-moment correlation coefficients were computed between averaged EMG amplitude of each muscle and force. Results indicate that the EMG amplitude of all four muscles is highly correlated with force during gripping a pen repetitively. Correlation coefficients are particularly high reaching 0.918 for FPB vs force, and 0.919 for EDC vs force. The values for 1DI and FDS are 0.812 and 0.711, respectively. In all subjects, the EMG of the four muscles showed a monophasic pattern. The burst of each muscle appeared simultaneously, which is characteristic of co-activation.

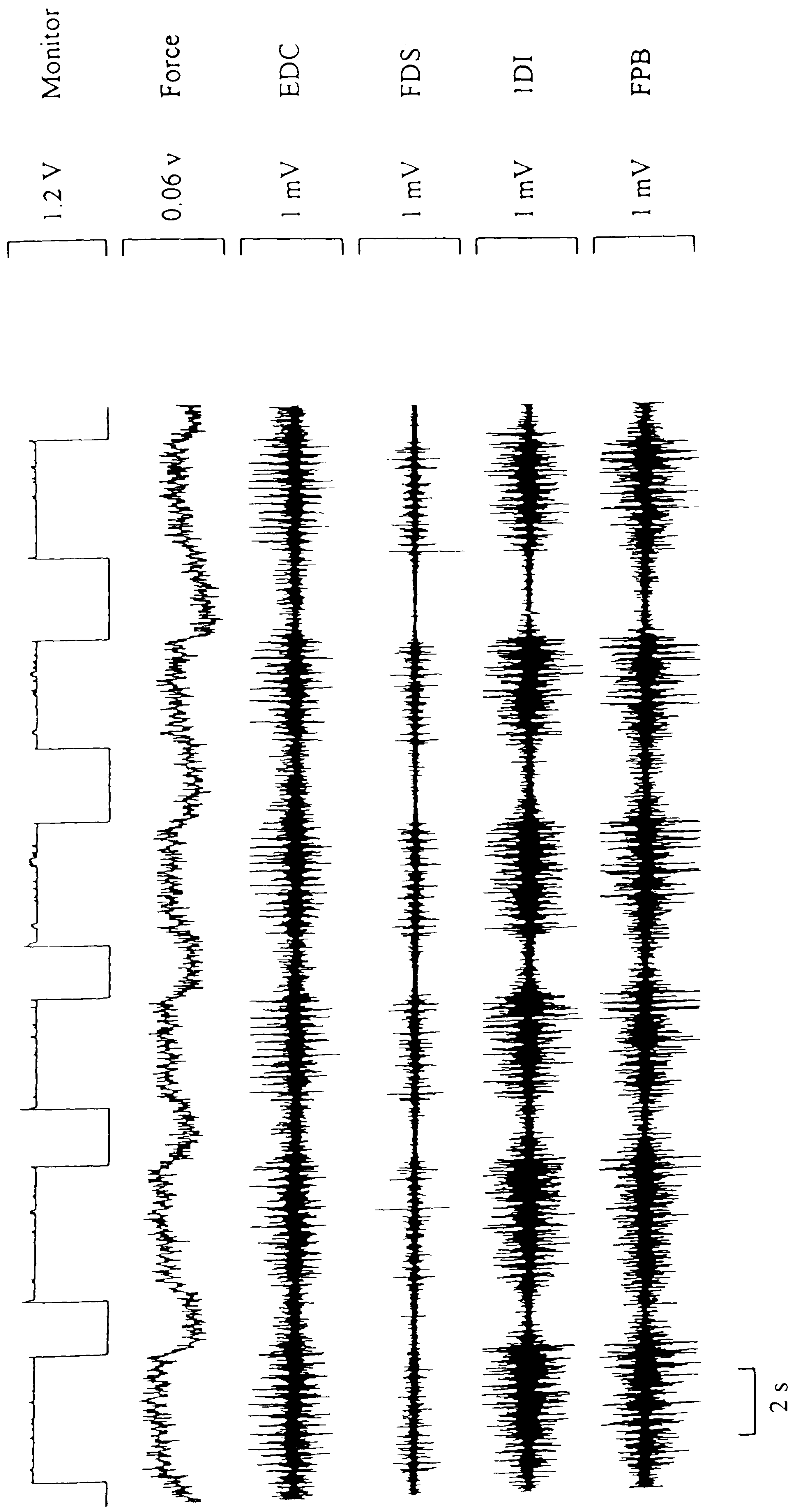


Figure 4.1. EMG activity recorded from four muscles while writing a nonsensical word ‘smegbred’ six times in succession. *Top trace:* monitor of pen-tip contact on aluminium foil during each word. *Traces 3-6:* raw EMG recordings.

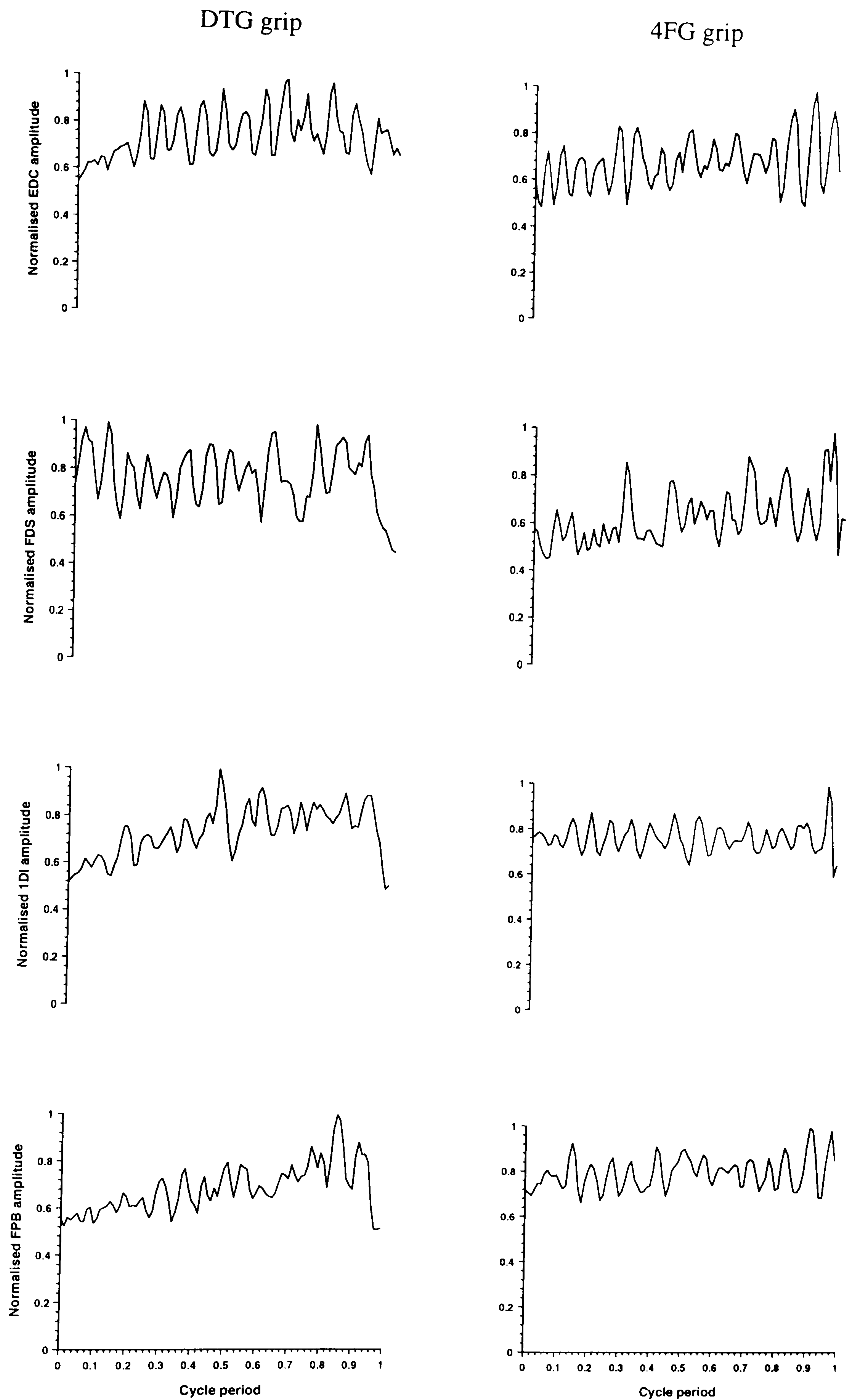


Figure 4.2 EMG phase diagrams of four muscles (indicated in Y-axis title) for writing ‘smegbred’ from 1 right-handed subject (KF) with DTG and 1 right-handed subject (MD) with 4FG. Each panel is an average over 10 successive repetitions. X-axis: normalised with respect to the cycle period; Y-axis: normalised with respect to the maximum amplitude.

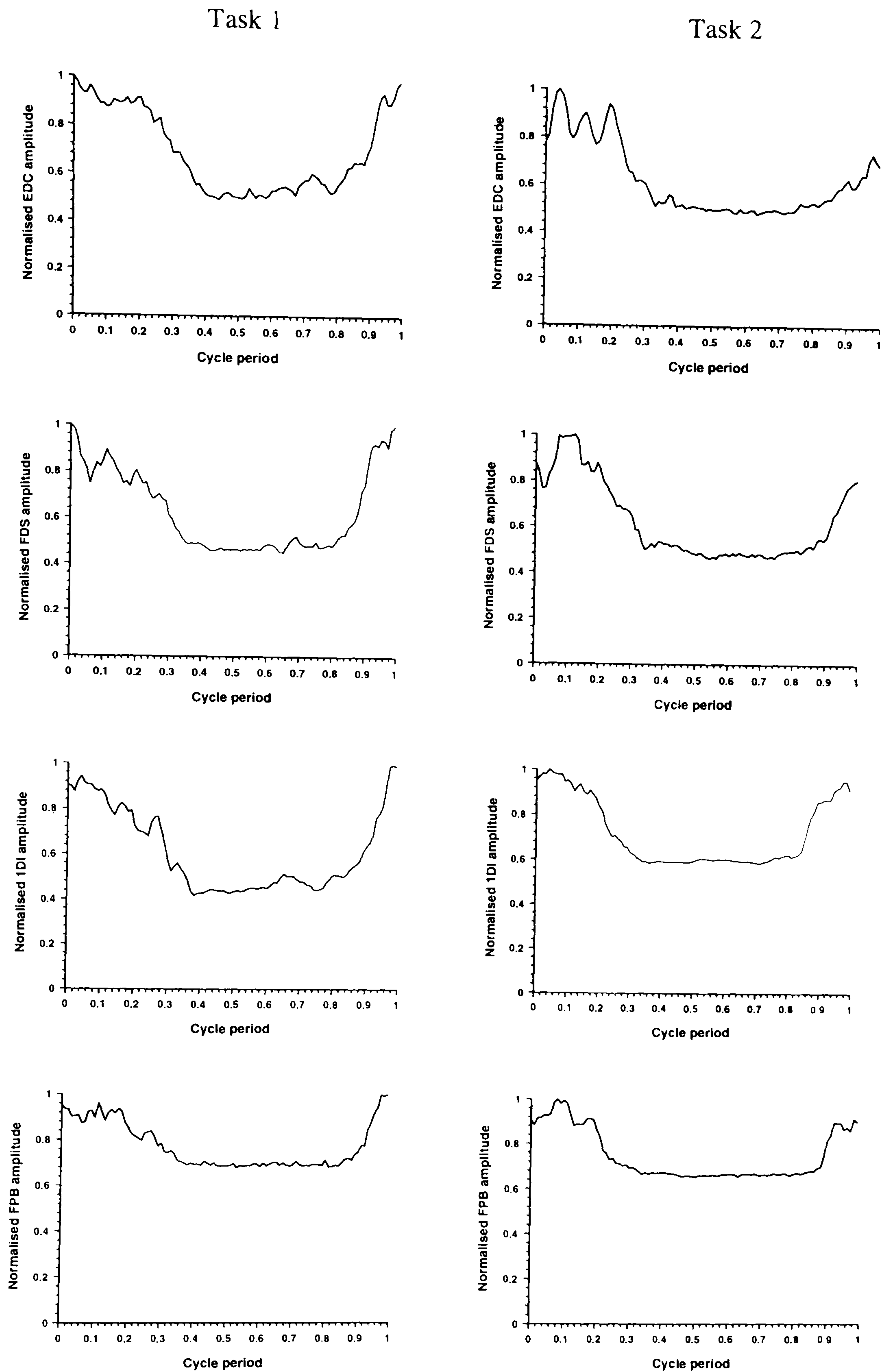


Figure 4.3. EMG phase diagrams of four muscles (indicated in Y-axis title) averaged over 10 repetitions in one left-handed subject with the DTG grip during 2 tasks. *Task 1:* holding a pen with usual pen-grip to press repetitively at 1 Hz with the force-pen tip on a cantilever brass beam; *Task 2:* repetitive opposition of thumb and index finger at 1 Hz, with the forefinger pressing on the force pen beam. X-axis: normalised cycle period; Y-axis: EMG amplitude normalised with respect to the maximum.

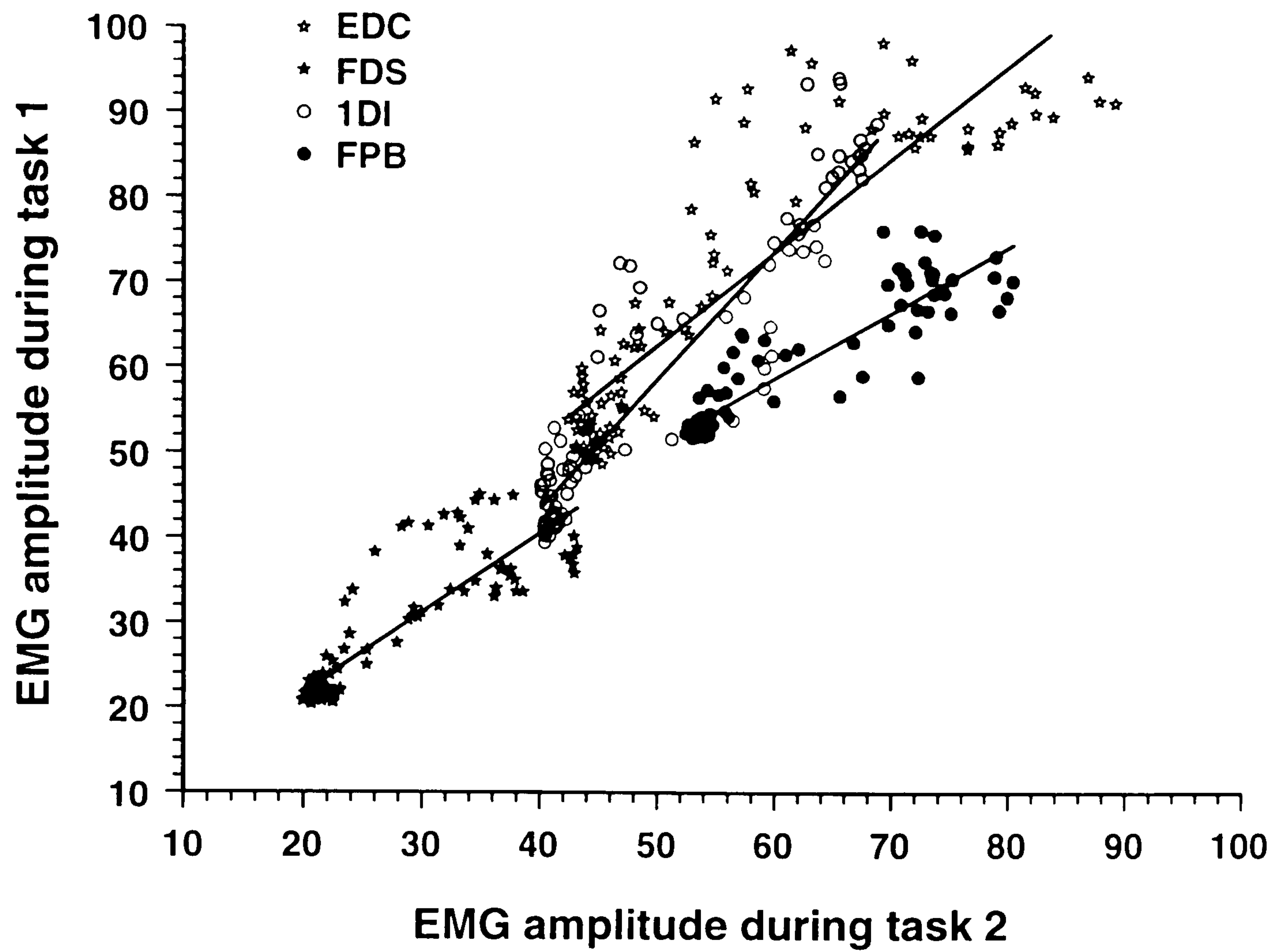


Figure 4.4. Correlation of EMG amplitude between 2 tasks from 4 muscles for the same subject shown in Figure 4.3. Correlation coefficients $r=0.886$ for muscle **EDC**, $r=0.859$ for **FDS**, $r=0.934$ for **1DI**, $r=0.920$ for **FPB**.

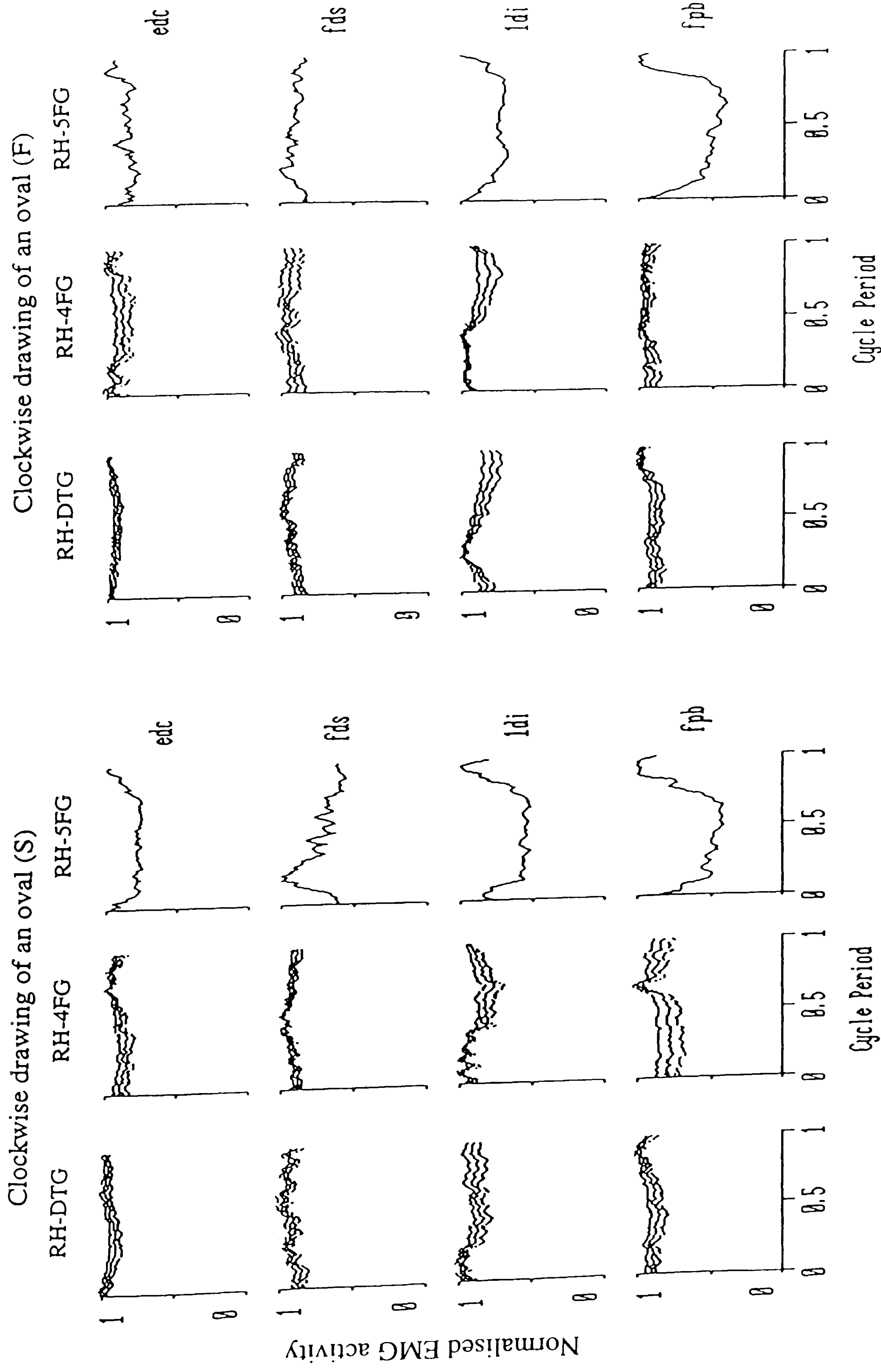


Figure 4.5. Averaged EMG phase diagrams for repetitive clockwise drawing of an oval shape sloping to the right. *Left*: pen-tip traced oval shape in a stencil (S); *Right*: oval was drawn freehand (F). Three different pen-grips are represented in each case: DTG (dynamic tripod grip), 4FG (four finger grasp), 5FG (five finger grasp). Each panel shows the normalised means for 10 successive oval drawings, averaged for 9 right-handed DTG, 5 right-handed 4FG subjects (*SEMs* shown for these) and 1 right-handed 5FG subject.

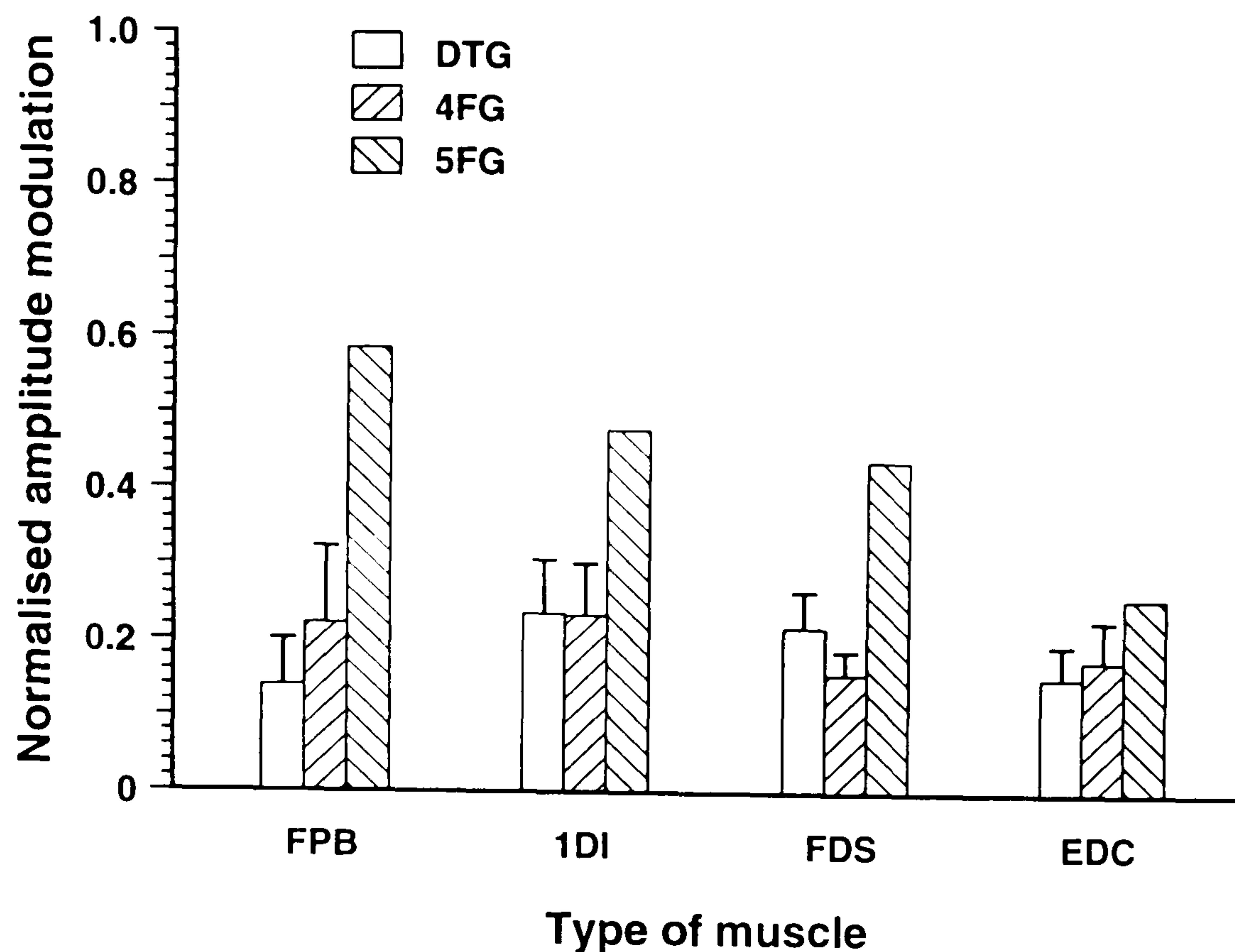


Figure 4.6. Normalised amplitude modulation of four muscles (indicated on the X-axis) during repetitive clockwise drawing of an oval shape sloping to the right. Drawings were performed using a stencil in three groups of right-handed subjects with different pen-grips: 9 with the DTG, 5 with the 4FG and 1 with the 5FG. Each bar represents the mean (+ s.d.).

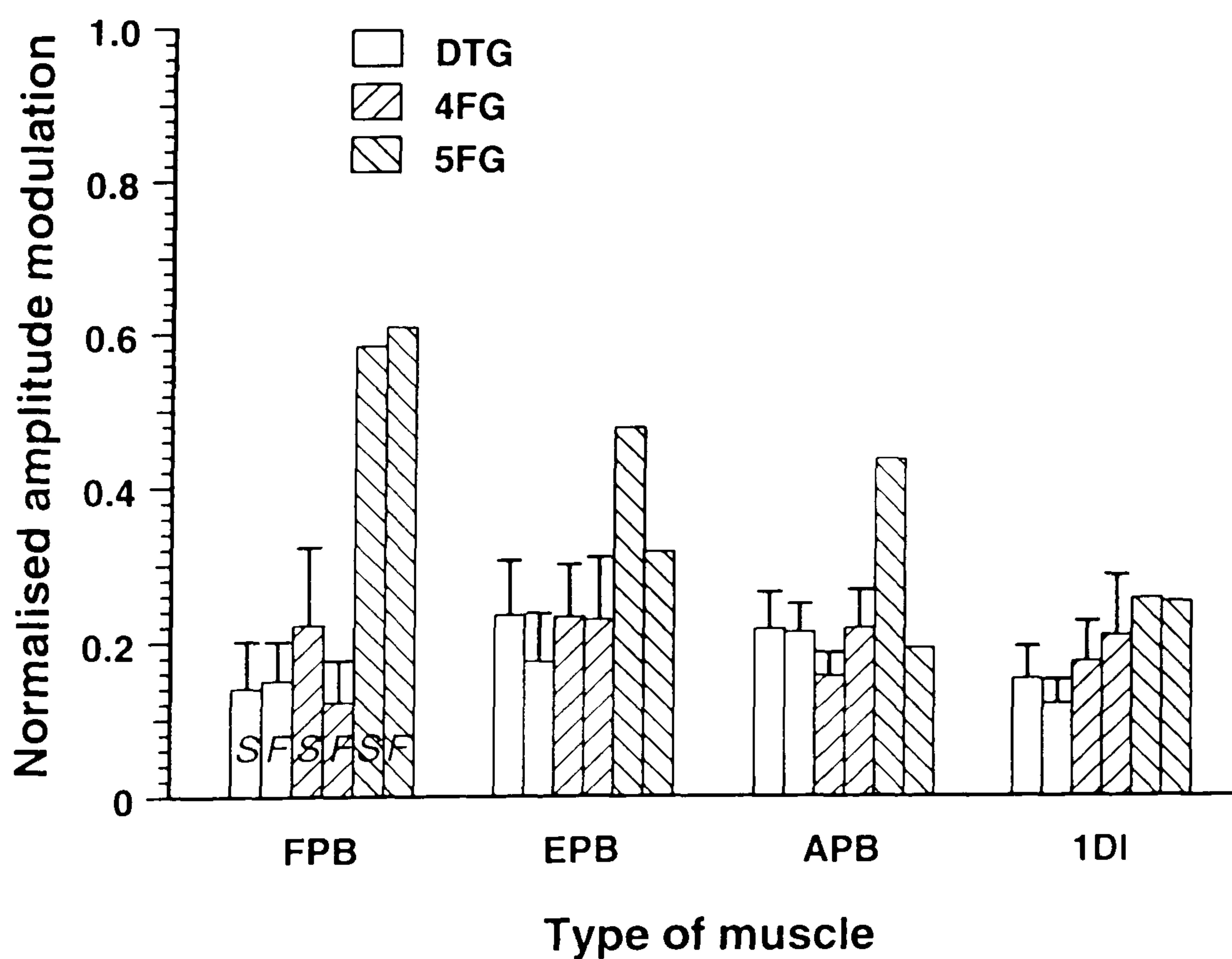


Figure 4.7. Normalised amplitude modulation of four muscles (indicated on the X-axis) during repetitive clockwise drawing of an oval shape sloping to the right. Drawings were performed using a stencil (S) and freehand (F) in three groups of right-handed subjects with different pen-grips: 9 with the DTG, 5 with the 4FG and 1 with the 5FG. Each bar represents the mean (+ s.d.).

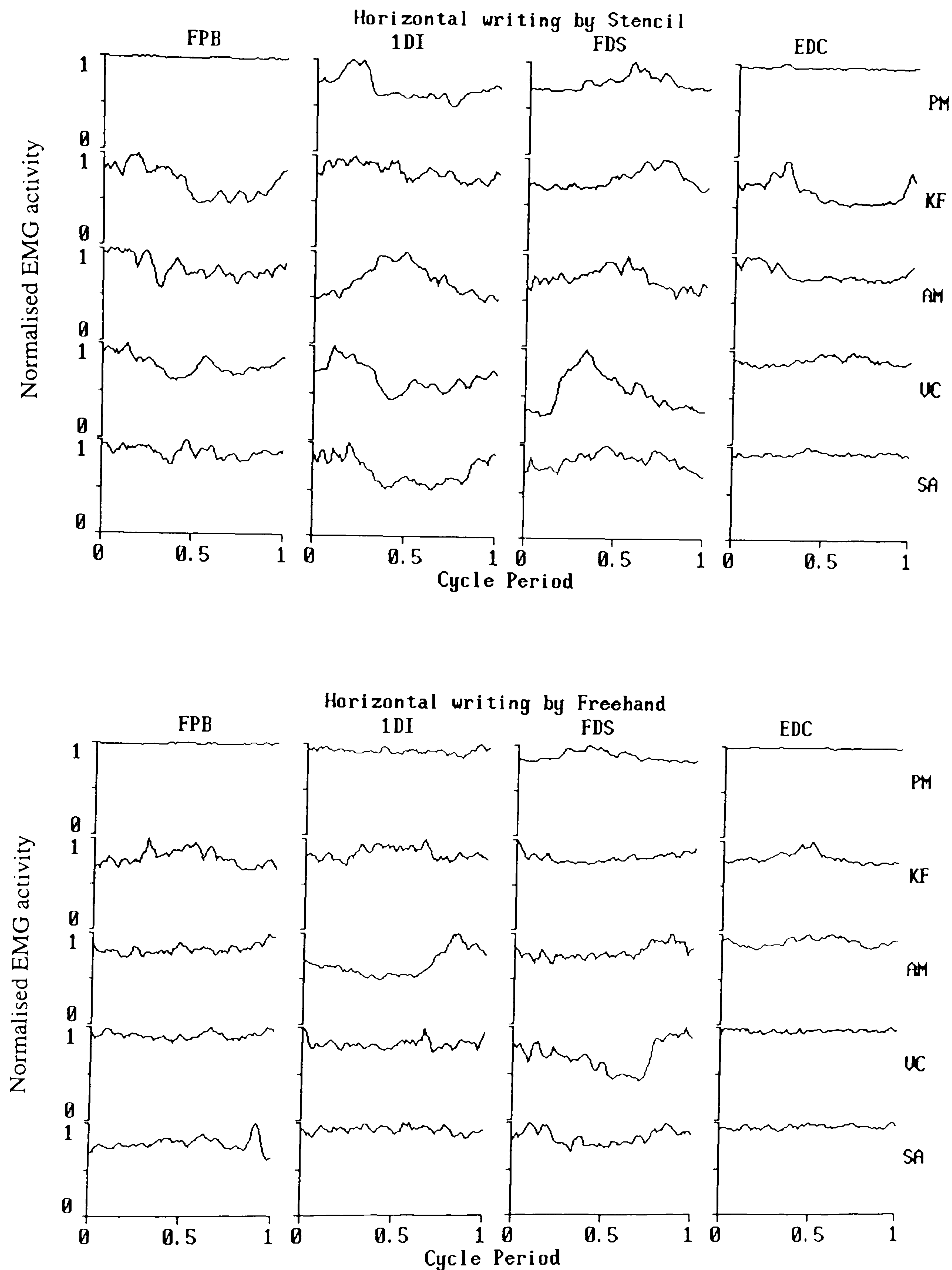


Figure 4.8. Individual EMG phase diagrams of four muscles for back-and-forth drawing a horizontal line in 5 right-handed DTG subjects, each averaged over 10 repetitions. *Top:* following the moving arm of a slide potentiometer (by stencil); *Bottom:* drawing the line freehand (by freehand).

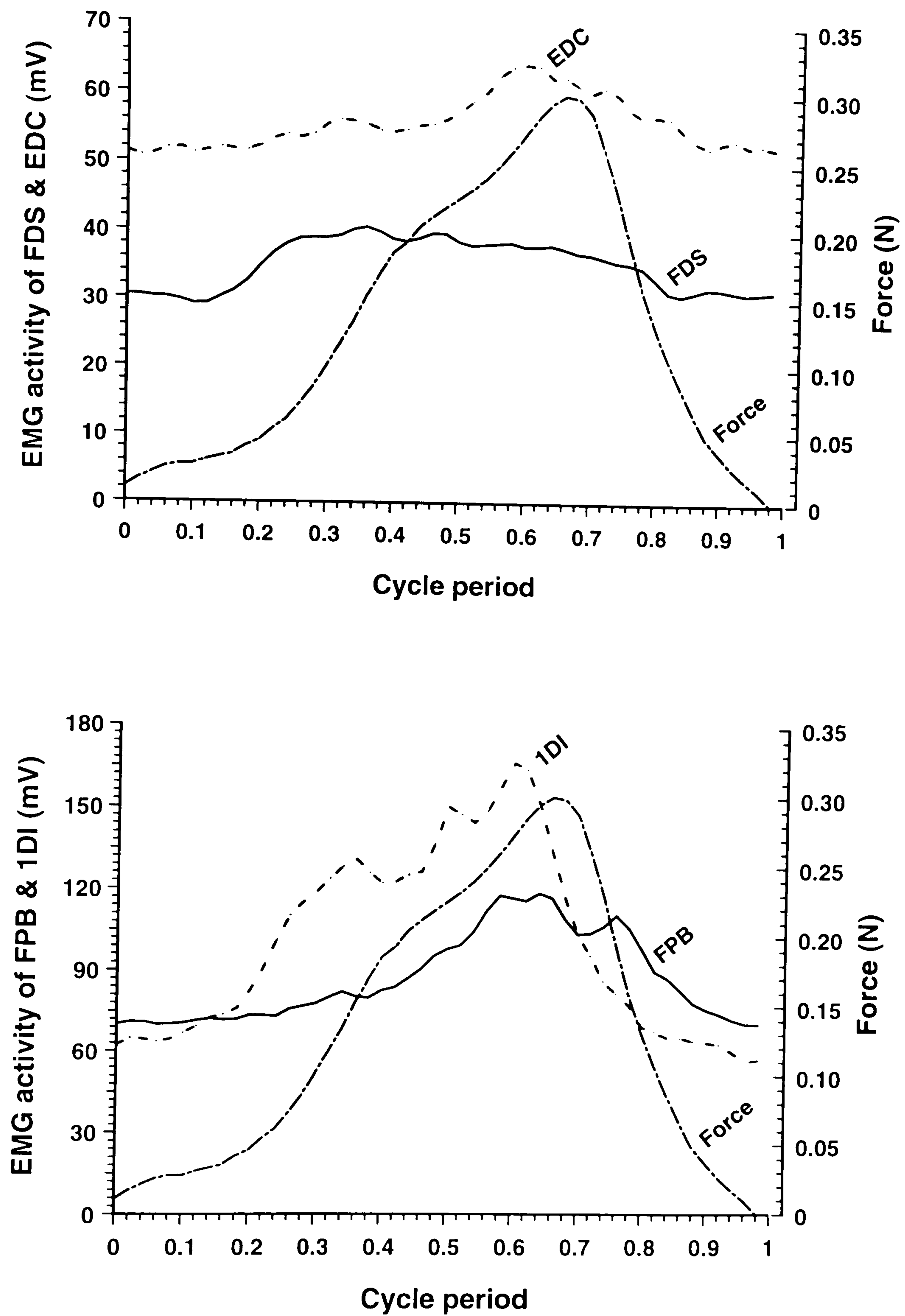


Figure 4.9. Averaged phase diagrams of EMGs and force over 10 repetitions for 6 right-handed subjects with the DTG grip during repetitive gripping of the force pen. *Top:* EMG activity of muscles FDS (*solid*), EDC (*dashed*) and force (*dash-dotted*). *Bottom:* EMG activity of muscles FPB (*solid*), 1DI (*dashed*) and force (*dash-dotted*).

4.4 Discussion

In this Chapter, the muscle activity patterns associated with various pen-grips have been presented in both right and left-handed subjects. The results have shown that handwriting EMG motor output appeared to be rhythmic (Figures 4.1 and 4.2), as has been generally accepted. EMG activities illustrated in Figures 4.1 and 4.2 display a series of ballistic movements during handwriting. In general, writing is composed of movement components exceeding 2 Hz. Based upon movement frequency, hand movement can be divided into two categories: slower movements and rapid single or rhythmic movements (Freund, 1986). Slower movements are performed under sensory guidance at rates below 1-2 Hz. Rapid rhythmic movements are commonly executed above 2 Hz. They include many skilled and learned movements. Writing is a typical example of this type of movements. As shown in the above figures, writing movement was executed around 3-4 Hz.

In Figures 4.3 and 4.4, it has been shown that the EMG modulation pattern of each muscle being studied appears to be very similar and highly correlated during repetitively squeezing a pen by two postures: the standard DTG grip and the opposition of thumb and the index finger. To explain this observation, we first of all compare these two postures. The only difference between them is that the middle finger is involved in the DTG grip, but not in the opposition task. In considering muscle function, muscle FPB, 1DI control thumb and the index finger movements, and muscle FDS, EDC flex and extend the four fingers. All four muscles contribute to the movements performed in both postures.

With respect to the motor output of different postures to hold a pen, results on the modulation patterns of all the muscles show that no significant difference exists between the DTG and the 4FG pen-grips during clockwise writing in both stencil and freehand writing. However, the amplitude modulation is much stronger in 5FG grip than in the other two grips, as illustrated in Figures 4.5 and 4.6. One possible explanation of

these observations are that the postures to hold the pen for DTG and 4FG grips appear to be very similar. Thumb or finger joints for these two types of pen-grip varied in approximately identical pattern in the execution of the tasks. Another explanation is related to muscle function, which has interpreted the modulation patterns of the DTG and opposition. In contrast, thumb and fingers for 5FG grip performed this task in a different way from DTG and 4FG. Finger movements in this uncommon pen grip involve a larger displacement. These results imply the function and significance of posture in the control of hand movements.

Apart from the above features, another characteristic difference is that the variation in depth and pattern of modulation appears greater when the pen-tip is constrained by a stencil or slide than in “freehand” drawing for each pen-grip (Figures 4.5 and 4.8). The movement trajectory in ‘stencil’ writing was defined by a stencil or slide. However, in order to produce the desired movement trajectory in freehand drawing, subjects used visual feedback and proprioceptive feedback to correct the position error on a moment to moment basis in the execution of the tasks. Therefore, the movement is somehow characteristic of open-loop in stencil writing, whereas the movement is closed-loop system in freehand writing. Moreover, comparison of phase diagrams in subjects with different pen-grips shows that the differences in ‘freehand’ writing tend to be more subtle than in ‘stencil’ writing, suggesting a more refined influence of proprioceptive feedback in regulating freehand writing tasks.

As described earlier in this thesis, the precisely controlled biomechanical forces exerted by thumb and fingers are essentially required for writing. Results illustrated in Figure 4.9 show that variations between muscle contraction and force exerted by the index finger are closely matched with each other. In general, muscle activities show a slight phase advance in comparison with the force due to the muscle contraction. Statistical analysis indicated that there is a strong correlation between EMGs and the force. Similarly, a recent study (Maier & Hepp-Reymond, 1995) reported that the intrinsic muscles and the long flexors of the index finger had a strong relation to force in

the precision grip. In contrast, the long extensors of the index finger did not show a correlation with force. Results obtained in the present study revealed a similar observation in the intrinsic muscles FPB, 1DI and the long flexor of the index finger, FDS, under dynamic conditions, but the opposite observation in the long extensor of the index finger, EDC. In summary, the movement patterns of handwriting are probably dependent on proprioceptive feedback, postures, muscles and limbs involved.

CHAPTER 5

PHASE-DEPENDENT REFLEX RESPONSES DURING REPETITIVE FINGER MANIPULATIVE TASKS

5.1 INTRODUCTION

Phase-dependent modulation of reflex responses to perturbation has been reported in both humans and other animals during locomotion (Forssberg, Grillner & Rossignol, 1975, 1977; Forssberg, 1979; Akazawa *et al.* 1982; Capaday & Stein, 1986, 1987; Belanger & Patla, 1987). These studies have examined the dependency of cutaneomuscular reflex, stretch reflex or H-reflex on the phase of the step cycle during different forms of locomotion, such as walking, running and standing, in the cat and the human. It has been first demonstrated that a stimulus applied to the dorsum of the foot of a cat, at the various phases of the step cycle during walking, elicited an excitation of the flexors during the swing phase and an excitation of extensors during the stance phase (Forssberg, Grillner & Rossignol, 1975). In humans, recent studies suggest that monosynaptic reflexes show a high degree of modulation during normal motor activities such as walking and standing, and the pattern of modulation can be specifically altered for different functional requirements of each motor task (Capaday & Stein, 1986, 1987; Stein & Capaday, 1988; Edamura, Yang & Stein, 1991; Brooke *et al.* 1995). This task-dependent modulation is regulated by the central pattern generators within the CNS as well as sensory feedback from the periphery (Stein, 1995).

There has been an increasing interest in the study of spinal reflex activity in the human arm in recent years (Caccia *et al.* 1973; Jenner & Stephens, 1982; Matthews, 1986; Evans, Harrison & Stephens, 1989, 1990). The advantage of employing the human arm rather than leg depends on the fact that particularly strong reflex changes can be evoked by stimulation of the fingers and thumb. These studies focus on the investigation of reflex mechanisms responsible for central-peripheral interactions in controlling the arm and finger movements. The stretch reflex has been widely studied in human arm, forearm and hand muscles (Darton *et al.* 1985; Matthews, 1989, 1993; Noth *et al.* 1991; Doemges & Rack, 1992a, 1992b). However, most of these studies were undertaken on muscles during constant contraction under static conditions. Very few studies have investigated modulation of the stretch reflex under dynamic conditions.

Exceptionally, modulation patterns of the stretch reflex were examined on human subjects during arm tracking movements in several studies (Dufresne, Soechting & Terzuolo, 1980; Johnson *et al.* 1991). None of these studies, however, have demonstrated stretch reflex modulation during rhythmic finger manipulations.

From the previous two paragraphs, although numerous studies have been reported in human and other animals, such studies under dynamic conditions have hitherto concentrated on the lower limb during locomotion, and many studies of reflexes evoked in human hand muscles by either electrical or mechanical stimulation were carried out under steady state conditions. The reflexes elicited during rhythmic finger movements have not yet been investigated. Moreover, new information has emerged concerning the way in which motor patterns are regulated by sensory feedback during rhythmic activity performed by the human hand. It has not yet been reported how the central pattern generator and sensory feedback interact in regulating the fingers and hands while performing repetitive finger manipulations related to handwriting.

The purpose of this study, therefore, was to evaluate the role of proprioceptive feedback in controlling skilled movements, by testing two hypotheses:

- (1) that the amplitude of EMG responses to mechanical perturbation is modulated in relation to the phase of the movement cycle (phase-dependency).
- (2) that the amplitude modulation is dependent on the task (task-dependency) during repetitive finger manipulatory tasks related to writing.

Preliminary results have been communicated to the Physiological Society Meeting and to the 11th Congress of the International Society of Electrophysiology and Kinesiology (Xia & Bush, 1996c, 1996d).

5.2 Experimental protocol

Experiment III

Type 1

Twelve healthy right-handed volunteers (5 males and 7 females), age ranged from 25 to 65 yrs and one writer's cramp subject (male, 19 yrs) participated in this experiment in order to assess the role of sensory feedback in the control of hand movements by testing phase-dependent reflexes evoked by mechanical stimulation applied at different phases of dynamic finger manipulatory tasks related to writing. All subjects held the pen with the standard DTG style required in one of the three tasks in which the three-way force pen was used.

Mechanical stimulation

Mechanical stretches were applied via a 12 mm disc on the moving end of the electromagnetic prod, driven by a power amplifier and a series of square wave pulses produced by a computer. Mechanical stimulus pulses, which lasted 100 ms and produced 0.5 - 1 mm displacement, were delivered at pseudorandom intervals ranging from 0.4 s to 1.2 s, equivalent to an average of approximately 1.45 Hz (Xia & Bush, 1996c, 1996d). This particular range was chosen on the basis of two considerations: (1) the minimum interstimulus interval being sufficient to include all possible reflex components; (2) obtaining a large enough number of stimuli delivered during recordings which did not cause any sign of fatigue. Mechanical stretches were applied to three sites, including the lateral side of the PIP joint of the index finger, the index finger pad and the pen-tip, depending on the tasks performed (see Experimental procedure). Application of stimulation during three tasks are shown in Figure 2.2.

Experimental procedure

Prior to recording, subjects' maximal voluntary force (MVF) were measured under three conditions associated with each task being performed. Three reproducible

readings were taken to obtain a consistent maximum in each condition as described here. Subjects sat on a height-adjustable chair with both hands on the table, (1) abducting as hard as possible with the lateral side of the index finger PIP joint pushing against a 12 mm diameter hard rubber disc on a cantilever beam with strain gauges bonded to it; (2) pressing down maximally on the disc with the index finger pad on the same cantilever; (3) squeezing the force pen as hard as possible. The MVFs from the index finger were recorded from each subject during measurement.

Subjects performed a standard protocol incorporating three rhythmic tasks, following a 'metronome' pulse at 1 Hz for 3 minutes in each task, whilst monitoring on an oscilloscope the force exerted by the index finger of the right hand. The three tasks included:

- (1) *Finger abduction/adduction*: abducting/adducting the index finger repetitively at 1 Hz speed, almost isometrically between two force limits (6% and 12% of MVF), with the lateral side of the PIP joint pressing against a 12 mm disc mounted on a force transducer in series with a stiff electro-mechanical prodder (Pye-Ling vibrator);
- (2) *Finger press*: pressing up and down with the tip of the index finger on the prodder at 1 Hz, keeping within the same force range;
- (3) *Pen-tip*: squeezing with a dynamic tripod grip the three-way force pen, so as to vary the force exerted by the index finger cyclically between 10% and 20% of MVF, whilst holding the pen-tip on the prodder with a nearly constant force of about 10% of maximum downward pressure. This 'pen-tip' manoeuvre was performed at each of three frequencies: 1, 2 and 0.5 Hz. During these experiments, a short period rest was taken between recordings to avoid the incidence of muscle fatigue.

During the performance of each task for three minutes, mechanical stimuli (100 ms in duration and ca. 1 mm displacement) were simultaneously delivered via the prodder at pseudorandom intervals of 0.4 - 1.2 s in the various phases of the movement cycle. Recordings were also made for 30 s while subjects performed the same manoeuvres without any mechanical stimulation. These were recorded in order to

subtract the baseline EMG activity from stimulated recordings in later analysis. For comparison with the dynamic conditions, responses to similar stimuli were also recorded under static state during the 'pen-tip' task, at three levels of constant isometric contraction. A constant pressure equivalent to 10%, 15% or 20% of MVF was maintained by the index finger on the prodder for two minutes each. These levels of contraction could be held for a few minutes before any sign of fatigue occurred.

The changes in resultant force produced by the index finger (or pen-tip) and prodder in each task, and also by the index finger on the pen in the 'pen-tip' task, were digitised along with surface EMGs recorded by paired electrodes simultaneously from four hand muscles: flexor pollicis brevis, extensor pollicis brevis, flexor digitorum superficialis and 1st dorsal interosseous.

Type 2

This experiment was conducted on 4 healthy right-handed subjects (3 males and 1 female) aged between 28 and 32 years. The experiment was designed to test the dependency of the cutaneomuscular reflex (CMR) elicited by electrical stimulation of the index finger on the phase of the cyclical 'finger abduction/adduction' movement. EMG recordings were made from one muscle only, the 1st dorsal interosseous of the dominant hand.

Electrical stimulation

Single electrical stimuli with pulse width 200 μ s were delivered from a constant current stimulator at 3 Hz (constant interstimulus interval) via a pair of ring electrodes. They were attached on either side of the PIP joint of the index finger for digital nerve stimulation. The cathode was positioned proximal and the anode distal to the PIP joint. In addition, the earth (reference) electrode was placed near the metacarpophalangeal joint around the index finger. Perceptual threshold was determined by gradually increasing the stimulus voltage until the subject reported that he could just feel each

stimulus distinctly. Stimuli were then applied at twice threshold for perception while each subject performed the repetitive 'finger abduction/adduction', which lasted for 2 minutes under both steady and dynamic conditions. This intensity of stimulation was chosen as it did not cause any unacceptable discomfort to the subject, and elicited a sufficiently large EMG response to be easily identifiable after a short period of averaging. Electrical stimuli were delivered at different phases of the finger abduction/adduction during rhythmical movement. The movement was performed at half the frequency of the stimuli, thereby ensuring that one stimulus occurred during the abduction phase and one during the adduction phase. For comparison with this dynamic condition, the cutaneomuscular reflex response of the first dorsal interosseous muscle was also recorded while the subject maintained a steady isometric abduction of the index finger.

Experimental procedure

Subjects sat comfortably on a height adjustable chair, with dominant hand on a table. Each subject conducted the index finger abduction/adduction repetitively at 1.5 Hz, with the lateral side of the PIP joint pressing against a cantilever beam with a strain-gauge mounted as a force transducer. The force exerted by the index finger was displayed on the screen to the subject in order to produce a variable contraction level which was between zero and 25% of MVC. Stimuli were delivered 167 ms later than the auditory cues which the subject followed to start the abduction phase of the movement. Each subject managed to follow the audio cues precisely. As expected, two stimuli occurred in one movement cycle, one in each of the two phases, i.e. abduction and adduction phases. The recording lasted for a 2-min period which was acceptable to the subject. EMG from 1DI with the digital nerve stimulation was also recorded while the subject performed a sustained index finger abduction at a 25% of MVC contraction level for 2 minutes. The reflex responses under the static condition were compared with the responses recorded under dynamic conditions. The force trace was simultaneously recorded with the EMG signal in each task. It was used to identify the phase of the cyclical movement during repetitive manoeuvres.

5.3 RESULTS

Data presented here are summarised from twelve subjects. Some results were obtained from only eleven out of the twelve because one subject failed to perform the rhythmic movement at the required speed. Data from one writer's cramp subject will be discussed in Chapter 6. Results related to digital nerve stimulation were obtained from one of four subjects participating in the experiment, as no obvious reflex responses were elicited in other subjects.

Responses during constant force 'pen-tip' task

Reflex responses were evoked in each muscle by repetitive 'prod' stimuli while the subject gripped the force pen so as to maintain a constant force in the index finger equivalent to 10%, 15% or 20% of MVF. Typical responses elicited by mechanical disturbance applied at the pen-tip during 15% of MVF in one subject are shown in Figure 5.1. It was observed that EMG responses were elicited in all four of the muscles recorded from. In most subjects, the segmented or multiple EMG responses consisting of short- and long-latency components were evoked in muscles FPB and 1DI only. The first two components, reflecting short- and long-latency responses, were obtained in eleven of the twelve subjects. The first component is generally considered as the spinal stretch reflex as its latency is compatible with monosynaptic activation involving group Ia spindle afferents. The second component, which was first reported by Hammond in 1954, has a much longer latency.

Only the short-latency response was evoked in EPB and FDS in most subjects. For convenience, these two components were labelled as M1 and M2, following the convention of Lee and Tatton (1975). The mean latencies of M1 and M2 components, elicited in both FPB and 1DI muscles in response to the stimulus via the pen-tip, are compared in Table 5.1. As it was usually difficult to differentiate the end of the M1 from the beginning of the M2, the latencies listed in Table 5.1 were taken from the time of stimulus to peak time of the reflex. The amplitude of M2 was often smaller than that

of M1. This relationship was indicated by expressing the peak amplitude of M1 and M2 as ratio M2/M1, which was 0.79 ± 0.16 (mean \pm s.d.) for FPB muscle and 0.64 ± 0.19 (mean \pm s.d.) for 1DI muscle in eleven subjects. The results shown in the rest of Chapter 5 were based on only the short-latency reflex component.

Table 5.1. Mean latencies \pm (s.d.) of M1 and M2 components elicited in distal hand muscles FPB and 1DI in eleven healthy subjects.

Muscle	n	M1 (ms)	M2 (ms)
1DI	11	37.5 ± 2.9	66.8 ± 8.8
FPB	11	37.6 ± 2.7	53.8 ± 5.4

Figure 5.2 illustrates the latency of the short-latency stretch reflex from 12 healthy subjects (mean \pm s.d.) in a barchart diagram. In this case, the latency was measured from the time of the stimulus to the take-off point of the response. It is clearly shown that the two intrinsic muscles FPB and 1DI have longer latencies than the two extrinsic muscles EPB and FDS, which strongly suggested that muscle receptors were involved in the reflex behaviour. Statistical analysis using *t*-test indicated that the differences of the reflex latency between intrinsic and extrinsic muscles are statistically significant at probability levels of $p<0.0001$. The relationship between reflex latency for each muscle and body height, which is associated with arm length, was investigated in this study. The results obtained from the 12 subjects are summarised in Figure 5.3, which shows that the short-latency of the reflex responses from all four muscles increased linearly with body height. The correlation coefficients are 0.506 for muscle FPB, 0.784 for EPB, 0.650 for FDS and 0.607 for 1DI.

Reflex associated with dynamic movements

Figure 5.4 shows the EMG activities, force traces and random stimuli of six movement cycles during the ‘pen-tip’ task performed at 1 Hz for one subject. The four lower traces (1-4) illustrate the EMG recordings from four muscles: FPB, EPB, FDS and 1DI. The 3rd trace from the top (trace 5) shows the force exerted by the index finger on the force pen. The force signal from the prodder superimposed with applied stretches is shown as the top 2nd trace and the random stimuli pulses generated by the computer are shown on the top trace. It is clearly demonstrated that stimuli were delivered at various phases of each movement cycle at pseudorandom intervals. Usually, it was necessary to average at least 10 sweeps in order to identify and measure the response since the single cycle did not show much sign of the reflex. Figure 5.5 represents the averaged responses of four muscles in the same subject evoked by mechanical perturbation over a 3-minute period while squeezing the force pen. These responses were obtained by averaging all 260 stimuli applied throughout the 3-minute period rhythmic movement. The reflex responses elicited under these dynamic conditions were closely comparable with those recorded in the static state represented in Figure 5.1.

Phase-dependent modulation of reflex response during cyclical finger movements

The reflex responses shown in the above example (Figure 5.5) represent the average of all responses, no matter at what phase the stimuli occurred in the movement cycle. In order to examine whether the reflex responses were dependent on the cycle phase or not, responses were averaged separately for each of 8 or 16 equal parts or phases of the cycle period. The cycle period was divided into eight phases for the tasks ‘finger abduction/adduction’ and ‘finger press’, as when it was divided into 16 phases, no stimuli were obtained in one of 16 phases in two subjects during these two tasks; for the ‘pen-tip’ task, however, 16 phases were used. Usually 20-40 stimuli occurred in each of 8 equal phases within a 3-minute recording and 10-20 stimuli in each of 16 phases.

In most subjects, the responses were strongly modulated as a function of the phase of the movement cycle. The depth and pattern of modulation varied with both the muscle and the task, as will be described later. An example of the reflex modulation in each phase of the movement cycle during the ‘finger abduction/adduction’ task performed at 1 Hz for one subject is shown in Figure 5.6. The first phase covered the starting phase of abduction. The stretch reflex of muscle 1DI during ‘finger abduction/adduction’ task increased progressively during the abduction phase, reaching its peak value shortly before the background EMG activity reached its highest level. The reflex then decreased with the reduced EMG activity during the adduction phase. In this example, the reflex gain is clearly modulated in a phase-dependent way.

The reflex response was calculated by subtracting the unperturbed record from the perturbed one. The measurement was taken as the average EMG amplitude over the specified window on the subtracted record. Two examples of this procedure are shown in Figure 5.7. Phase 2 occurred in the early part of abduction when 1DI was active, whilst phase 7 occurred during the adduction phase where 1DI activity was relatively low. The top traces show the averaged 1DI responses of approximately 30 stimuli in phase 2 (left) and phase 7 (right). The averaged recordings when the muscle was unperturbed are shown in the middle part of the diagram for these two phases. The bottom traces illustrate the subtracted EMG responses in the corresponding phases. The size of the reflex was measured as the average EMG over a specific time period, which was specified as the duration between intersection points of response and the mean background EMG level (a 20 ms EMG average before the stimulus). This process was repeated for each phase of the full cycle. These measured values are plotted as a function of the phase in the movement cycle (Figure 5.8C). The corresponding EMG background level and the force signal from the prodger are plotted in Figure 5.8B and A, respectively. These indicate that the EMG shows a 1.5-division phase lead compared with force in this case. This reflects the contraction time of the muscle: it is well-documented elsewhere, and is often referred to as the electro-mechanical delay. The 1DI reflex responses in turn show a 1-division phase lead with respect to the background

EMG (Figure 5.8B & C). The amplitude of the 1DI response co-varied directly with the EMG activity level in this muscle. The correlation coefficient between the reflex and EMG activity within each phase of the cycle was 0.84. Such a close correlation between muscle activity and the reflex amplitude was also observed in the other tasks and muscles studied for other subjects.

Figure 5.9 is an example of a different, more complex task, the cyclical ‘pen-tip’ task, executed at 1 cycle per second. The reflex response amplitudes and EMG activity from muscle FDS for one subject are plotted for each of 16 equal divisions or phases. The FDS reflex reached the peak value one phase division before the peak of FDS muscle activity. In this instance, the force signal (upper graph), representing the pressure exerted by the index finger on the pen, showed a slight phase advance in relation to the background EMG activity of FDS in the unperturbed cycle.

The examples that have been illustrated here so far show that the responses increased approximately in parallel with the motor activity in the muscle. However, the opposite relation between reflex response and background EMG of 1DI muscle was observed in two subjects during ‘finger abduction/adduction’ task, which are shown in Figure 5.10. In these examples, the 1DI reflex response amplitude (or gain) was again strongly modulated, but the reflex strength varied inversely with the EMG activity. As in Figure 5.8, the EMG activity increased during the abduction phase and decreased during the adduction phase, but the reflex response of 1DI was now much smaller during abduction than during the adduction phase. In both examples, the reflex response reached a peak value 4 phase divisions behind the EMG peak value, that is half way through the movement cycle.

Task-dependent modulation of reflex gain during repetitive finger movements

In this part of the study, the reflex response amplitude and the mean level of background EMG at the time the reflex was elicited were plotted against each other. This analysis was employed to test whether the modulation of the reflex evoked by

mechanical stimulation is purely associated with the α -motoneurone excitation level during the dynamic manipulatory tasks. The relationships between the reflex response and the corresponding mean background EMG activity levels during the three tasks studied are shown in Figure 5.11, for two subjects; those for 1DI are shown in the upper plots and for FDS in the lower plots. The plots on the left (A and C) of Figure 5.11 show the reflex response plotted as a function of the mean EMG activity in the same phase as each response was elicited. Plots on the right (B and D) show the ratio of the reflex response to the mean EMG activity as a function of the phase in the cycle.

Using the difference between maximum and minimum to express the extent of modulation, the reflex of 1DI during ‘finger abduction/adduction’ task (109.57 mV) and ‘pen-tip’ task (91.52 mV) were modulated more strongly than during ‘finger press’. In association with the main function of muscle 1DI, which is to abduct the index finger, it is easier to interpret this reflex pattern. In Figure 5.11A, the size of the reflex response obtained during ‘finger abduction/adduction’ was much higher than during ‘pen-tip’ and ‘finger press’ tasks for the same amount of voluntary contraction. Figure 5.11C shows that the depth of modulation during the ‘pen-tip’ task is greater than the other two manipulations. In comparing the tasks ‘finger abduction/adduction’ and ‘finger press’, the reflex size appeared to be of a similar level even though the background EMG activity during ‘finger abduction/adduction’ showed a stronger contraction level than during ‘finger press’. In Figure 5.11B, it is evident that the ratio of the 1DI response to EMG activity is higher for ‘finger abduction/adduction’ than for the other two tasks. In Figure 5.11, diagram D shows the ratio between the FDS response and EMG activity during ‘finger abduction/adduction’ in each phase was lower than that during ‘pen-tip’ and ‘finger press’ tasks. This could be related to FDS muscle function during the tasks being performed.

These results suggest that the reflex was not simply a passive reflection of the pre-existing voluntary contraction level. Figure 5.11A and 5.11C also show that the pattern of reflex modulation between the three tasks involves a difference in the slope of

the regression line, indicating a difference in the sensitivity of the reflex response. The values for the slope are given in the figure legend. The slope of 1DI was highest in ‘finger abduction/adduction’ (Figure 5.11A), as 1DI plays an important role in performing this manoeuvre. For FDS, the slopes were much higher during the ‘pen-tip’ and ‘finger press’ tasks than during ‘finger abduction’, as FDS is more important in performing the former two tasks than the latter one. Thus, the pattern of reflex modulation differs between tasks for the same muscle, and between muscles in a given task. The modulation pattern of reflex gain illustrated in Figure 5.11 was observed in most subjects, except in the small number of subjects who demonstrated negative correlations between the reflex gain and the pre-existing muscle activity, or who showed a lower degree of modulation in a given muscle during a certain task. The results suggest that a complex reflex mechanism may be associated with these observations.

Effect of movement frequency on modulation of reflex gain during repetitive ‘pen-tip’ task

We have analysed the task-related reflex modulation during a variety of repetitive finger manipulatory tasks. What will be the effect of dynamic movement speed on the pattern of phase-dependent modulation of the responses to vibratory stimuli in a given task, e.g. the repetitive ‘pen-tip’ task? Figure 5.12 shows the modulation in the reflexes of FDS and 1DI as a function of the phase during the ‘pen-tip’ task executed at frequencies of 0.5, 1 and 2 Hz for one subject. The difference between maximum and minimum amplitudes was used to indicate the extent of modulation, which was very close between the three frequencies for the same muscle in this subject. The extent of 1DI modulation was greater than that of FDS modulation in all three cases. This pattern of modulation between movement frequency and muscle was also observed in other subjects.

Before the depth of modulation was averaged across subjects, the modulation was normalised to the maximum value to account for the large variation of reflex amplitude between individual subjects. The average was done across only ten of the

twelve subjects, as one subject was not able to perform the ‘pen-tip’ task at the required speed, and the other did not perform this task at the two extra frequencies. Mean values at the three frequencies obtained from ten subjects are shown in Figure 5.13, in which normalised depth of modulation is plotted as a function of the movement frequency for muscles FDS and 1DI. There were no significant differences between different movement frequencies in each muscle. However, the extent of phase-dependent modulation for 1DI during the pen-tip movement performed at 0.5 and 1 Hz was significantly greater than for FDS under the same condition ($p < 0.05$). These results suggest that the movement speed had little effect on the pattern of reflex modulation elicited by mechanical perturbation during repetitive finger movement.

Phase-dependent modulation of the cutaneomuscular reflex in the first dorsal interosseous during repetitive finger movement

So far, we have shown that the stretch reflex elicited in hand muscles including 1DI is highly modulated with respect to the phase of the movement cycle during repetitive finger manipulations. Dependency of the cutaneomuscular reflex of 1DI on the phase of the cycle during rhythmic index finger abduction/adduction was examined in this study. The reflex evoked under steady finger abduction at 25% of MVC contraction level was recorded in comparison with the reflex elicited under dynamic conditions. Figure 5.14 shows an example of the average 1DI reflex response to repetitive electrical stimulation during sustained finger abduction for one subject (bottom), as well as a 6-second excerpt of the rectified EMG signal and the steady state force produced by the index finger (top).

In this part of the study, we focused on the investigation of the reflex modulation under dynamic conditions. During rhythmic finger abduction/adduction, 1DI activity displayed periodic EMG bursts at the same frequency as the movement performed. The force trace shows an approximately sinusoidal curve indicating the rhythmic muscle contraction. Due to the muscle contraction, the EMG activity generally reached the peak level prior to the force. Figure 5.15 shows the rectified 1DI EMG recording and the

accompanying force trace during the movement, as well as the average EMG and force for one full movement cycle, averaged over 180 cycles. Stimuli were delivered at 3 Hz whereas the movement was performed at 1.5 Hz. Two stimuli, therefore, were expected to occur within each movement cycle, as illustrated in the bottom panel of Figure 5.15. The stimulus occurring on the rising phase of the repetitive finger abduction/adduction produced an obvious EMG response while the muscle was contracting, whereas the stimulus on the falling phase did not cause any EMG change. This observation indicates that the cutaneomuscular reflex of 1DI muscle is modulated with respect to the phase of the movement cycle during cyclical finger abduction/adduction. However, cutaneomuscular reflex responses were not easily identified in the 1DI muscle of other subjects.

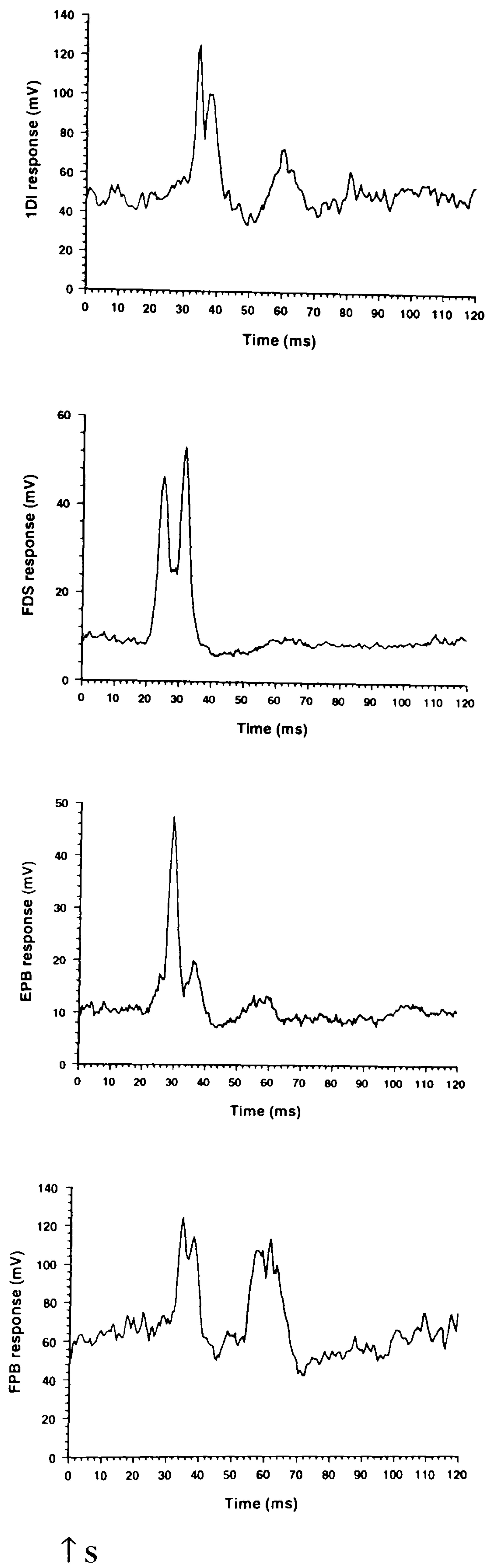


Figure 5.1. Reflex responses evoked in four muscles (indicated in Y-axis title) during constant 'pen-tip' task at 15% MVF for one subject (LL). Stimuli applied at time zero. Each trace represents an average over 170 sweeps.

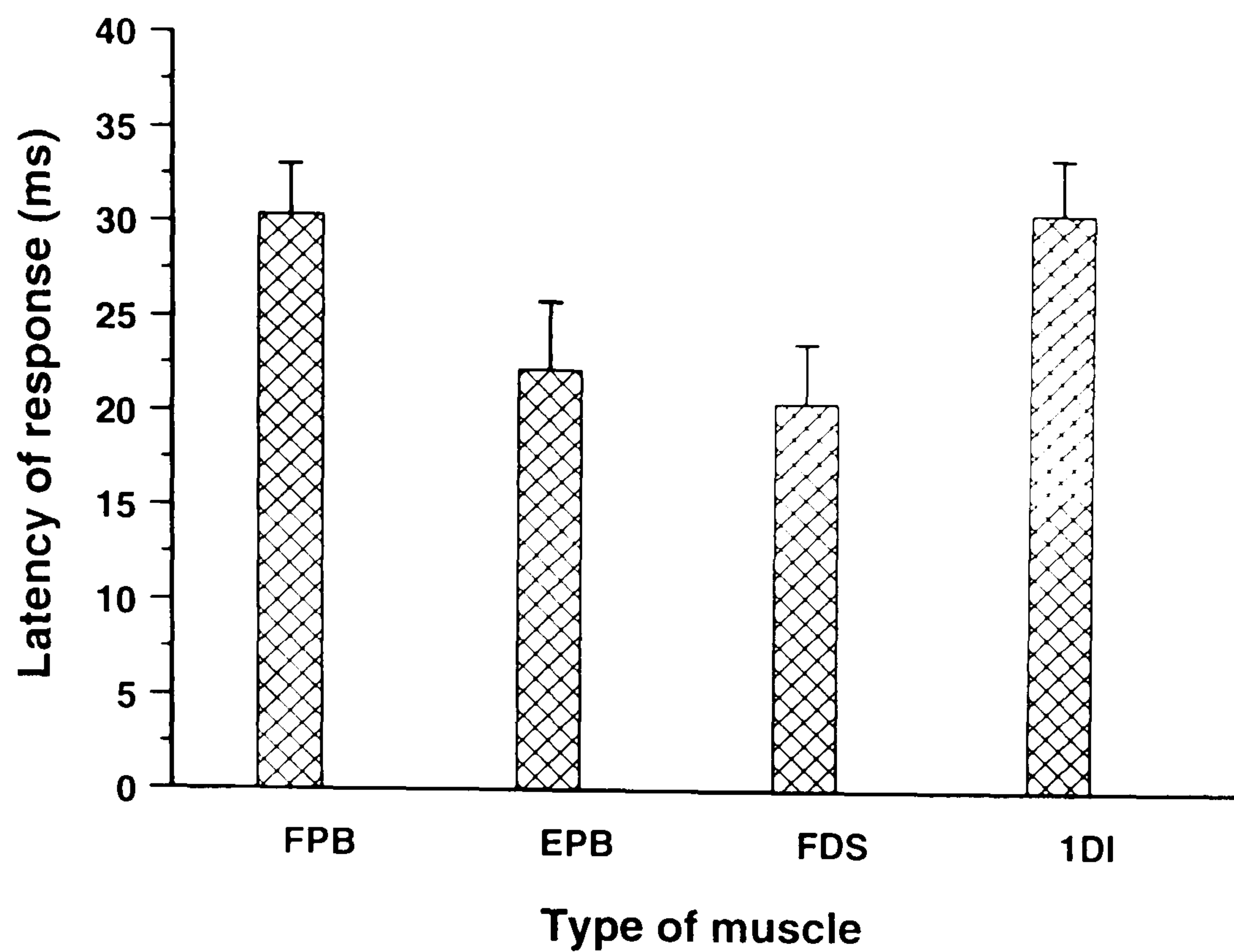


Figure 5.2. Latencies of M1 reflex component from 4 hand muscles indicated on X-axis during constant pen-tip task. Each column represents the mean (+ s.d.) averaged in 12 subjects.

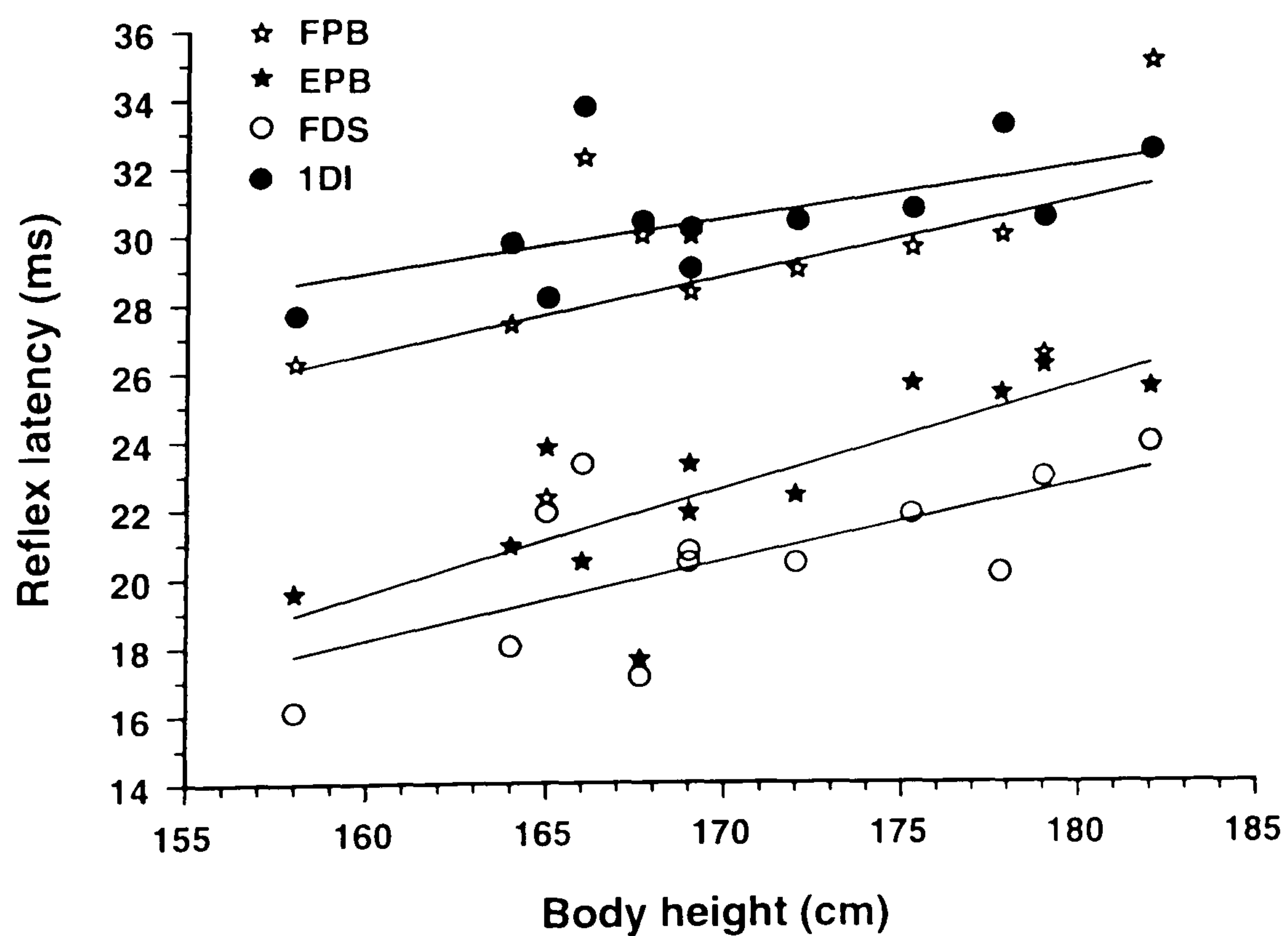


Figure 5.3. Correlation between the reflex latency of four muscles and body height in 12 subjects. **FPB:** $r=0.506$; **EPB:** $r=0.784$; **FDS:** $r=0.650$; **1DI:** $r=0.607$.

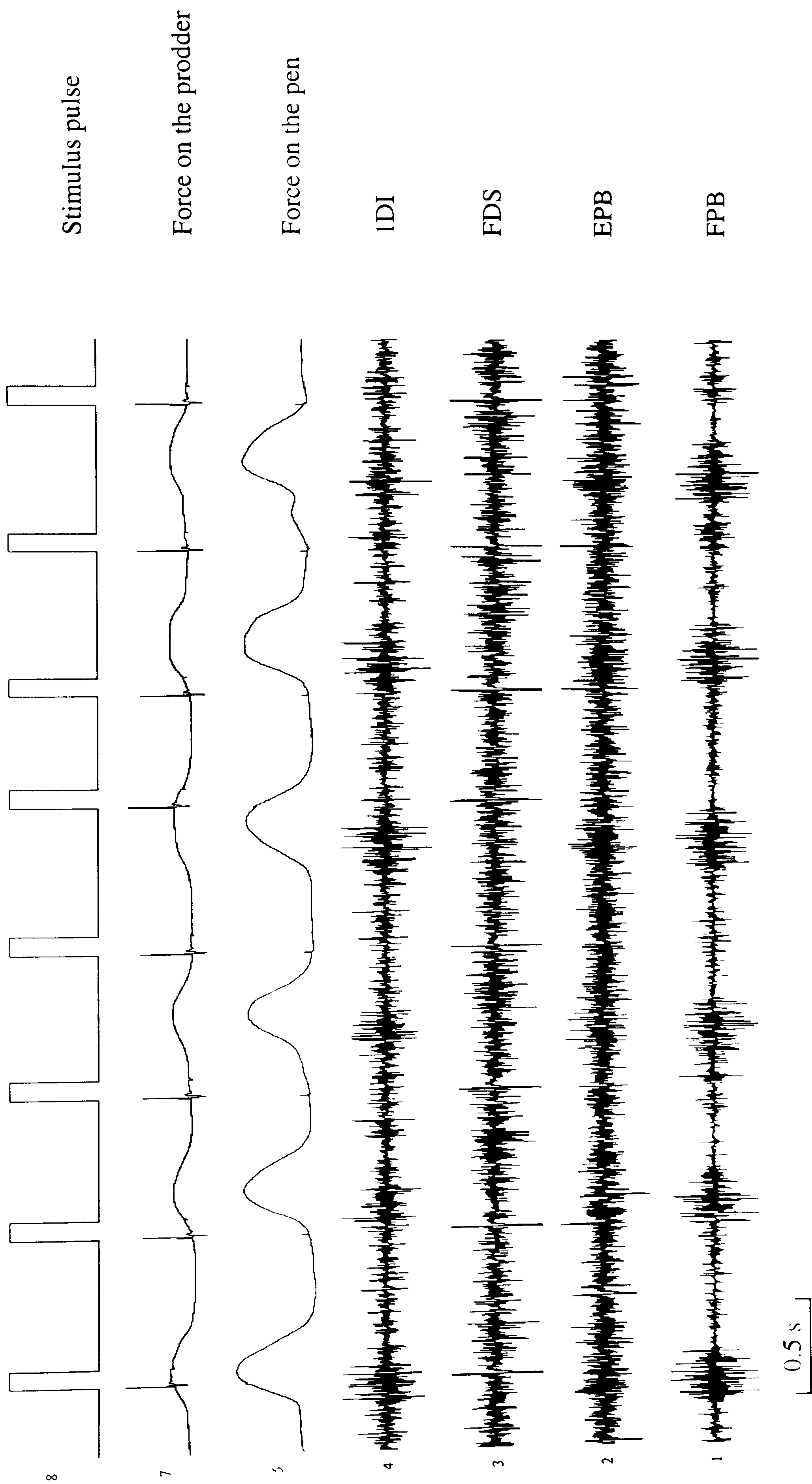


Figure 5.4. EMG recordings from four muscles and force traces indicated above during rhythmic pen-tip task for one subject. Mechanical stimuli were applied at pseudorandom intervals, as shown on the top two traces.

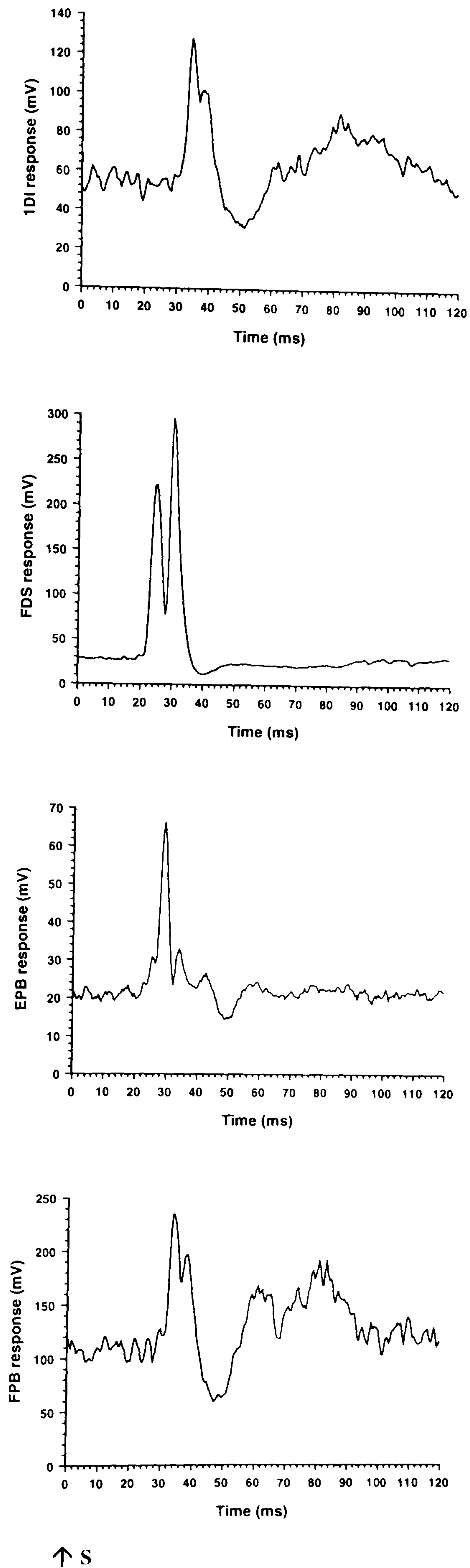


Figure 5.5. Reflex responses elicited in four muscles during repetitive pen-tip task in the same subject shown in Figure 5.1. Stimulus was applied at time zero. Each trace represents an average of all 260 stimuli over a 3-min period, irrespective of the phase in which the stimuli occurred.

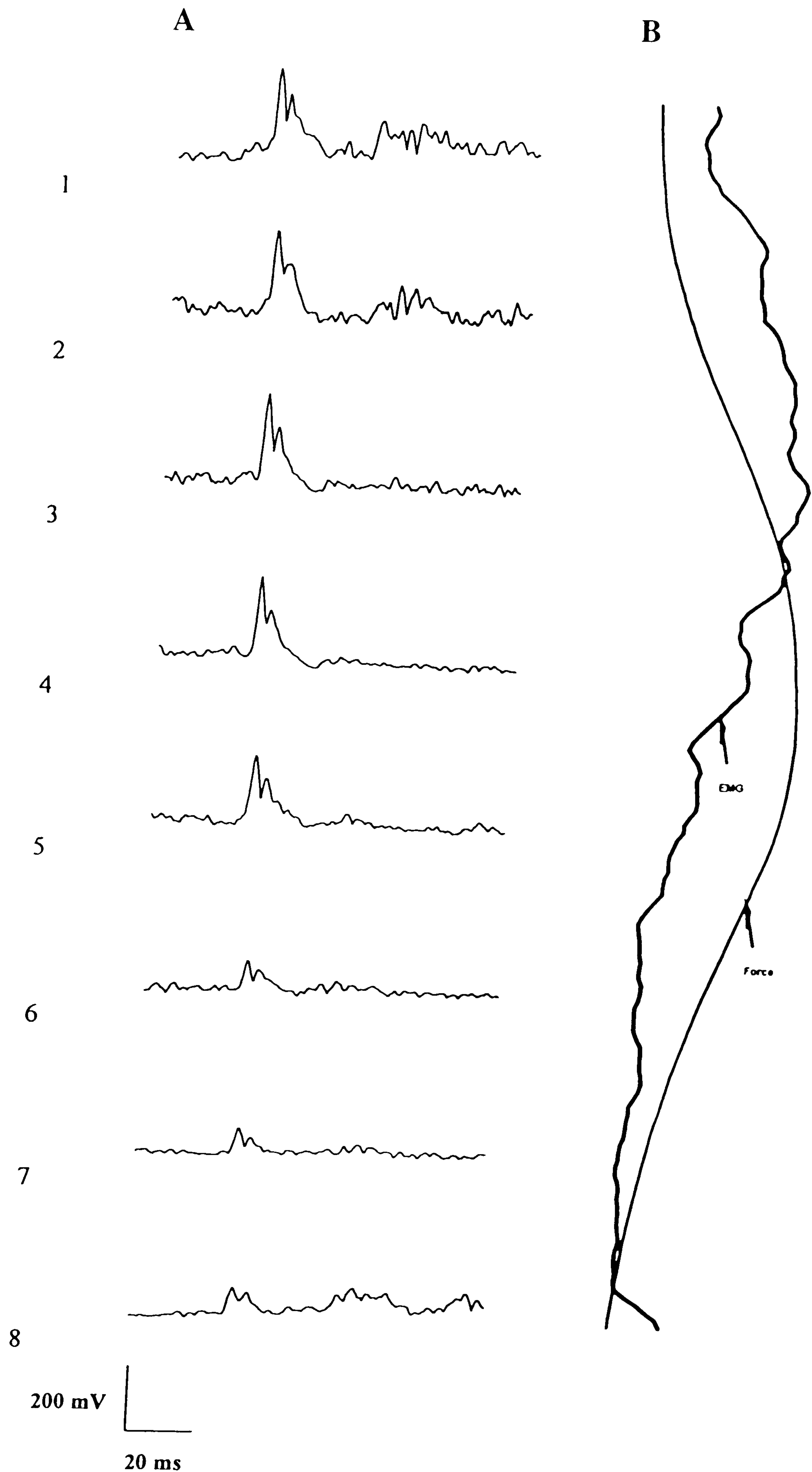
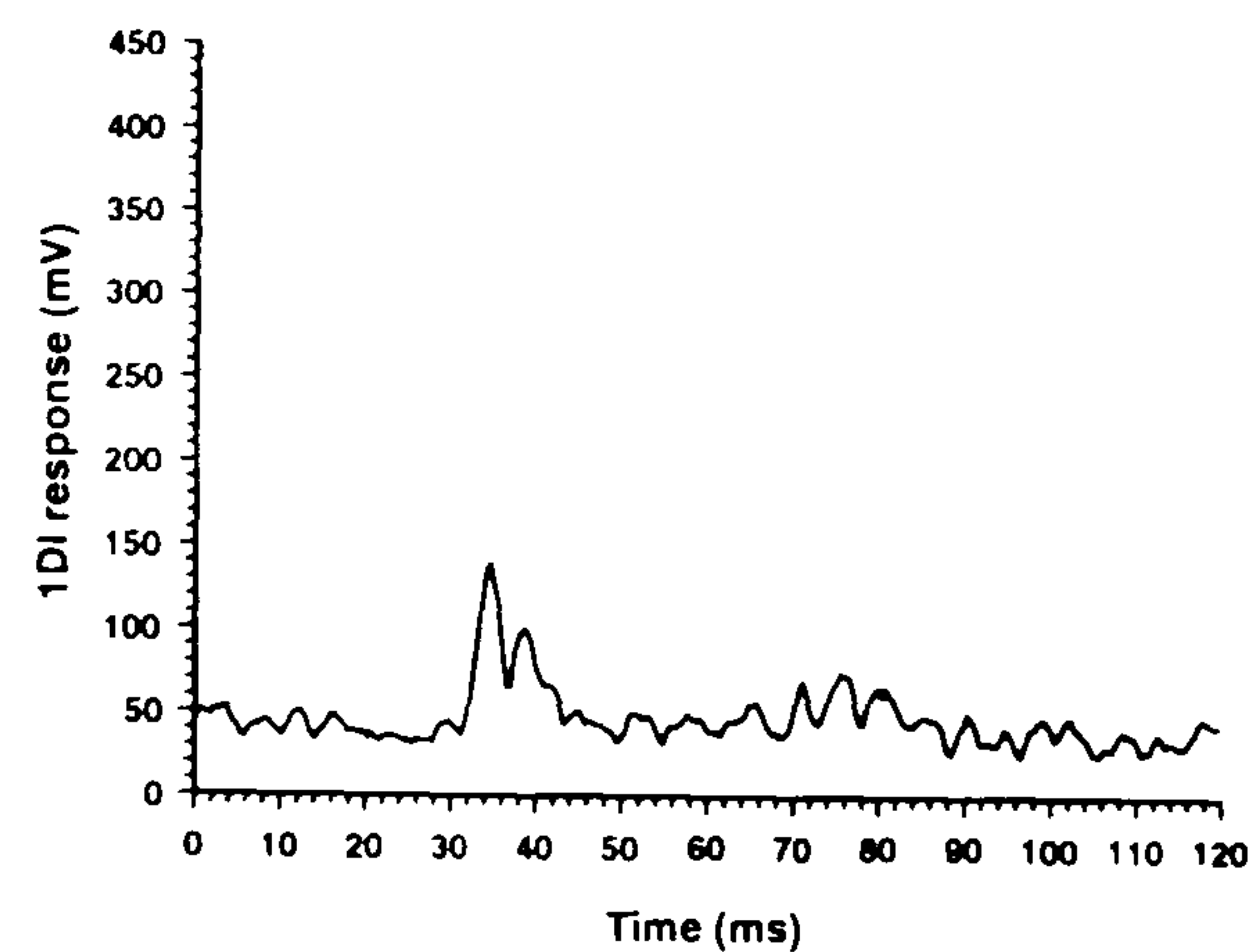
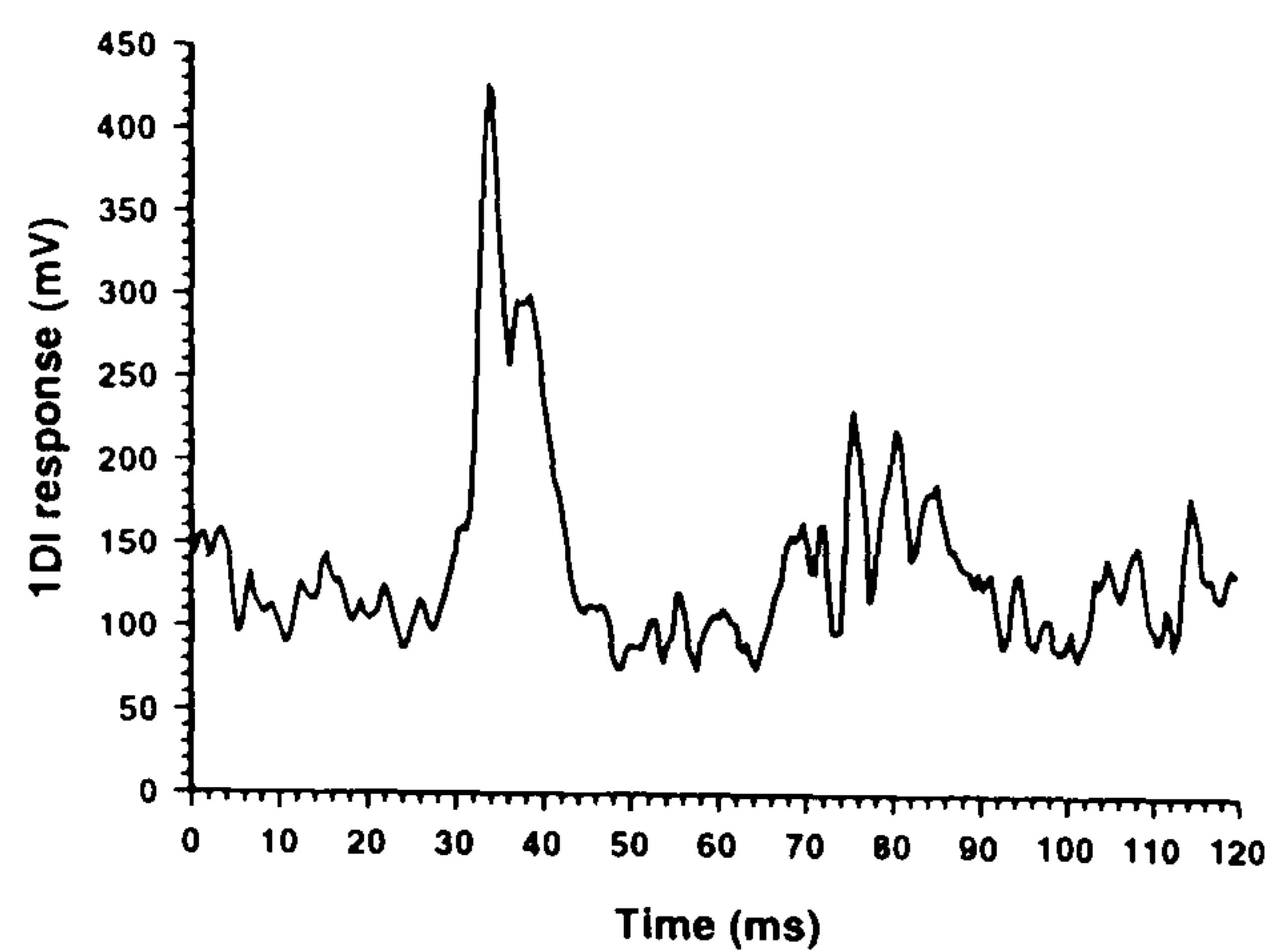


Figure 5.6. A: Reflex modulation of 1DI stretch reflex at various phases of the movement cycle during the finger abduction task. Each trace represents the average of 24-48 stimuli occurring in the phase indicated on the left (the full movement cycle being subdivided into 8 phases). **B:** Average background EMG and resultant force, aligned vertically in relation to the 8 equal phases represented by the 8 traces in (A). Vertical height: cycle duration; force and EMG amplitude: arbitrary units (increasing towards the right).

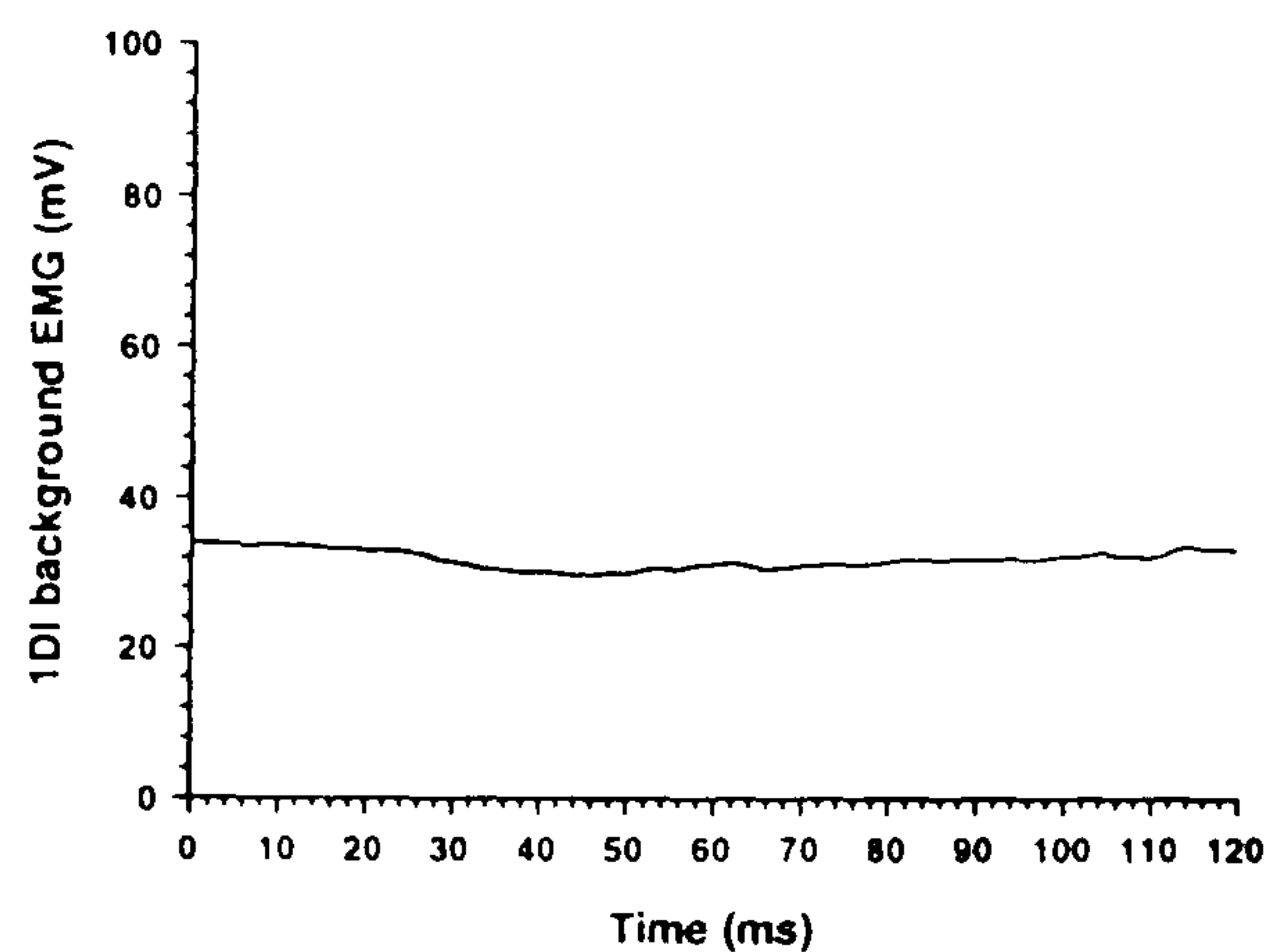
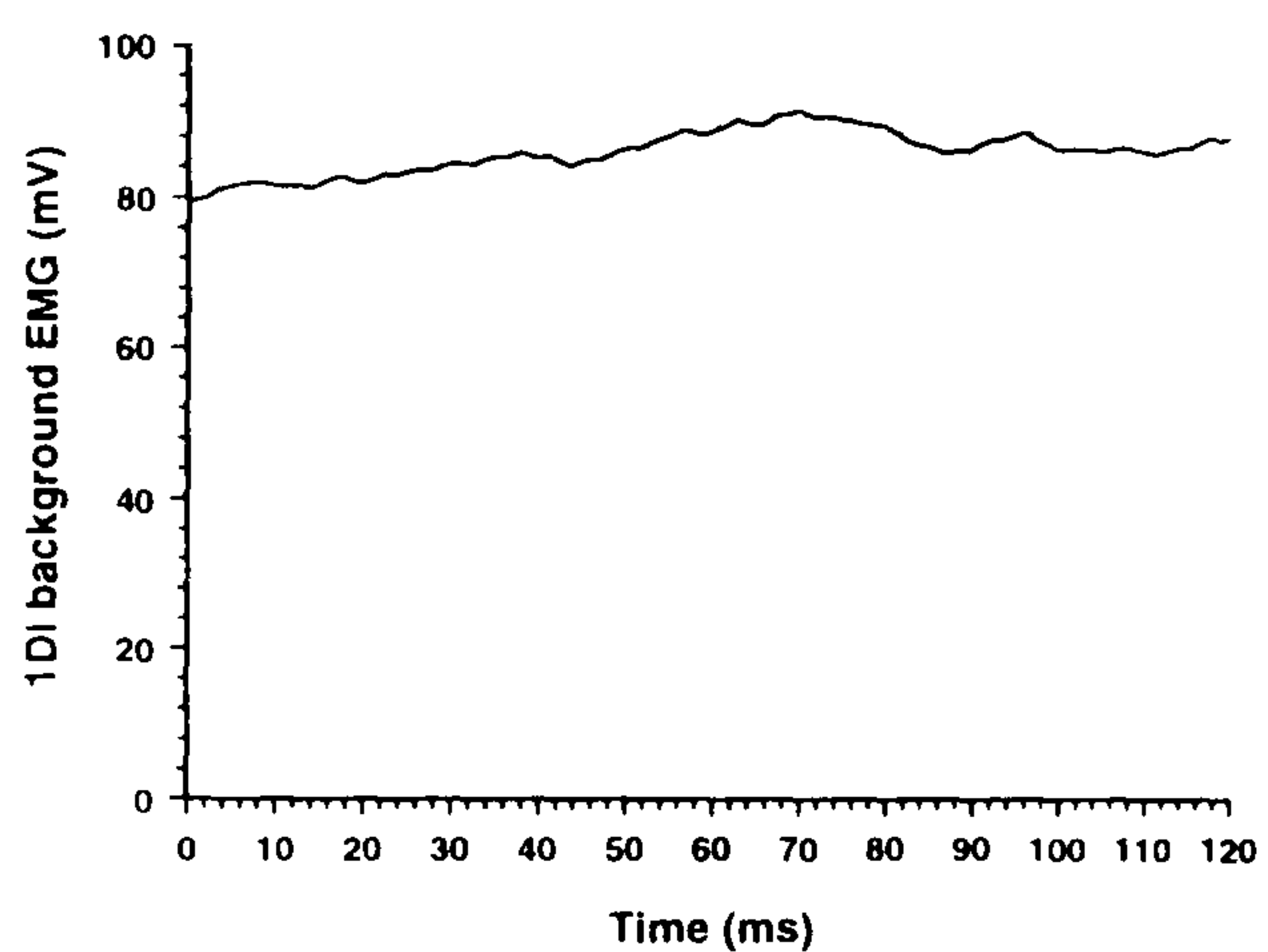
Phase 2

Phase 7

Averaged responses



Unperturbed averages



Subtracted responses

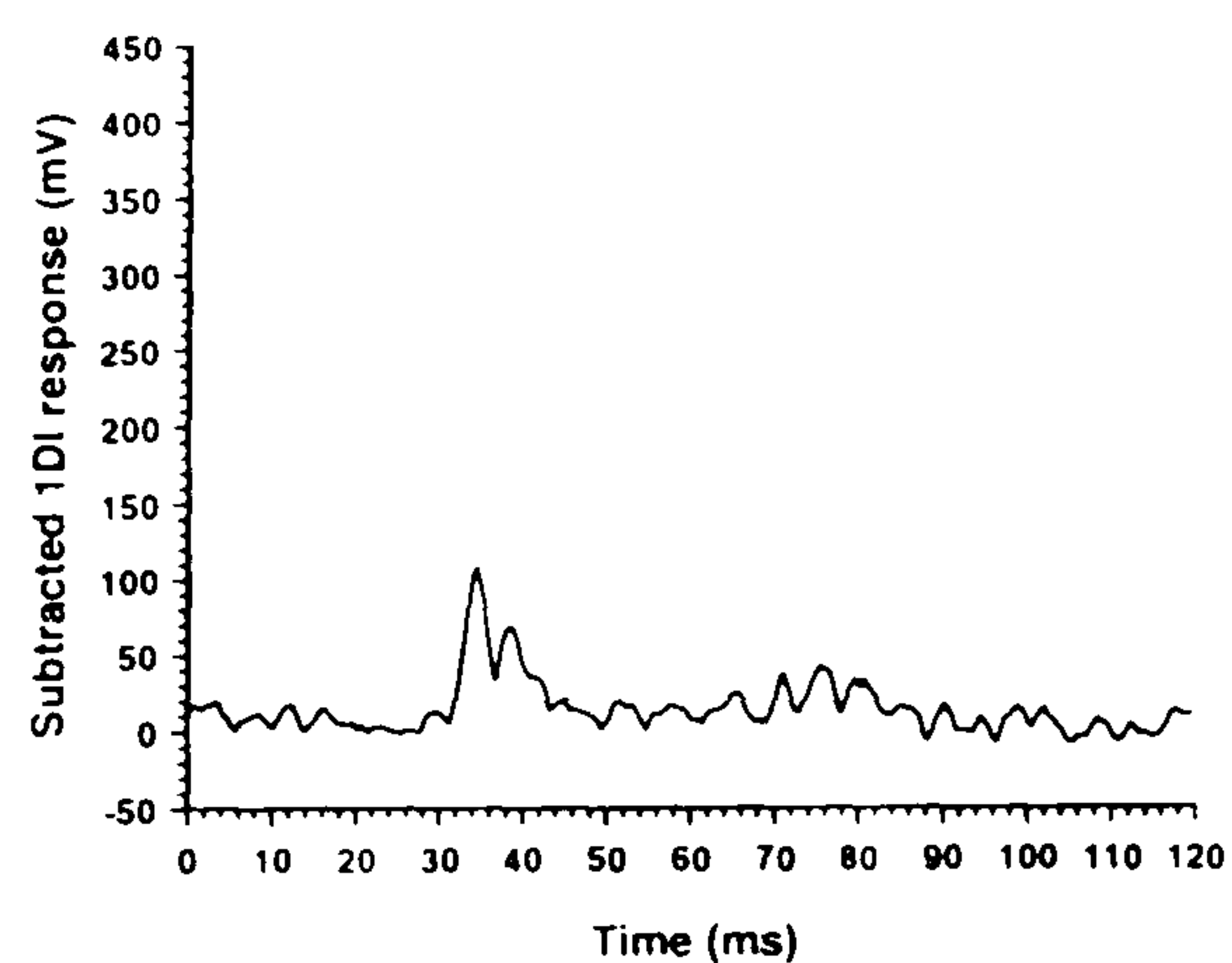
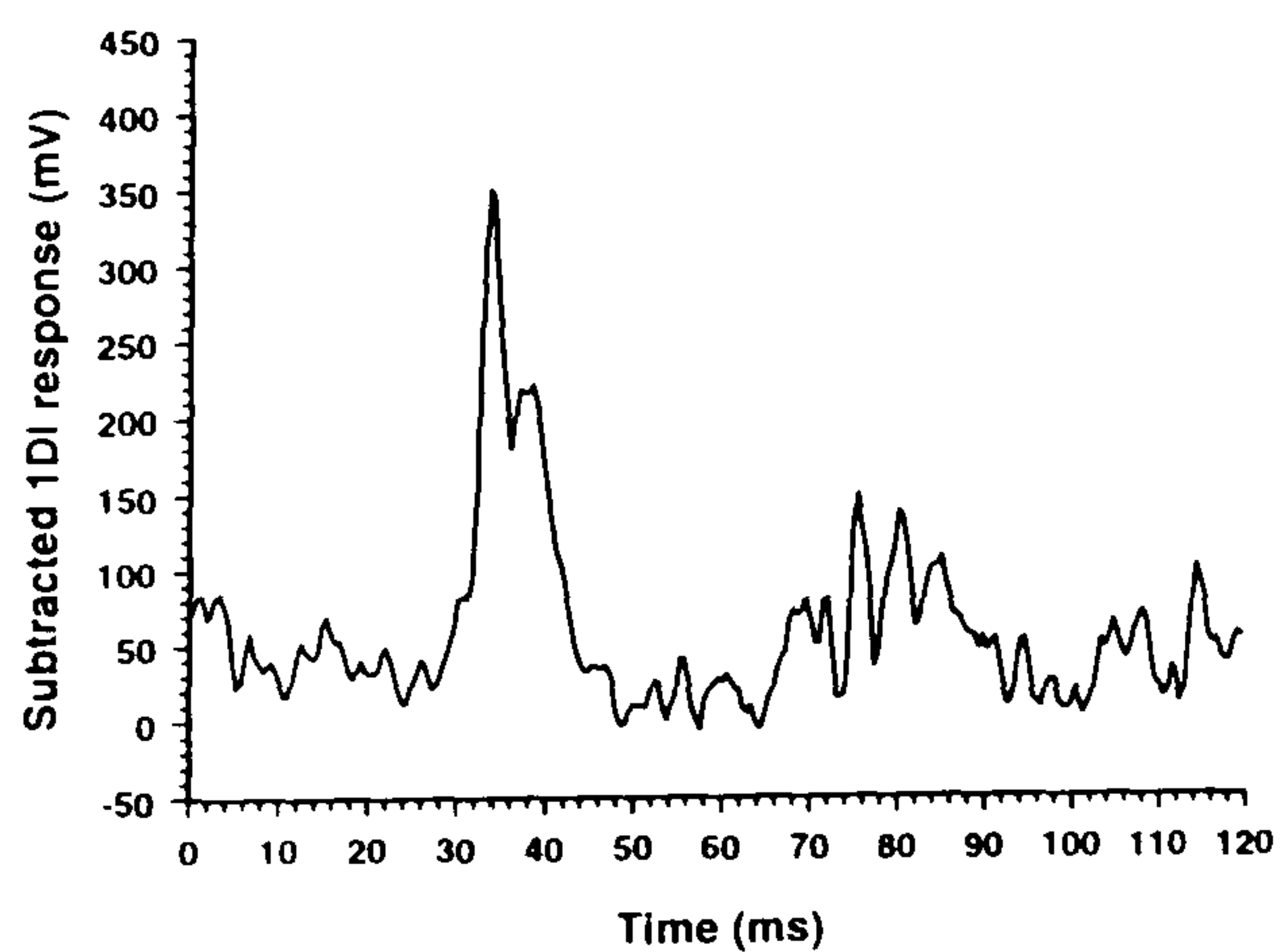


Figure 5.7. 1DI responses in phase 2 (left) and phase 7 (right) during 'finger abduction/adduction' for the same subject as shown in Figure 5.6. *Top:* averaged responses of 32 stimuli in phase 2 and 29 stimuli in phase 7. *Middle:* averaged non-stimulated recordings. *Bottom:* subtracted EMG responses.

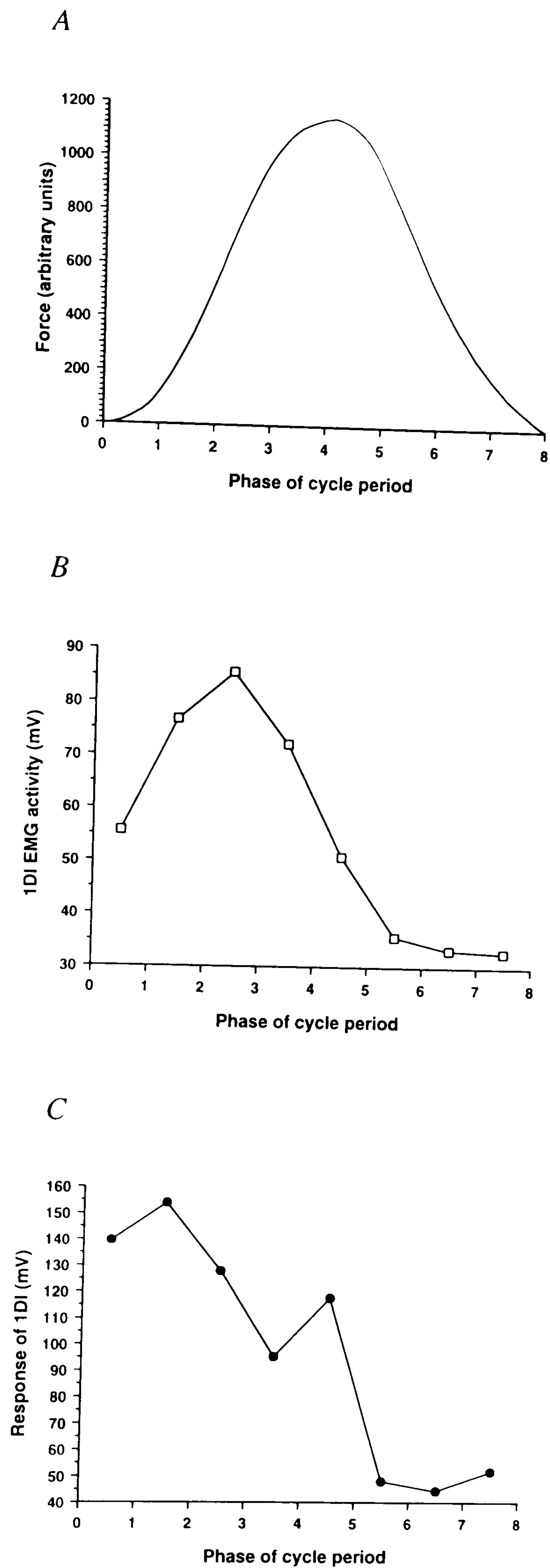


Figure 5.8. Relation between amplitudes of mechanically evoked 1DI reflex responses and phase of the repetitive 'finger abduction/adduction' movement, compared with background EMG activity and resultant force. *A*: Averaged force trace over 30 cycles of unperturbed 'finger abduction/adduction'. *B*: Averaged EMG activity of 1DI for 30 cycles. *C*: Averaged reflex responses of 1DI to repetitive 'prod' stimuli for the 8 equal phases of the 'finger abduction/adduction' task.

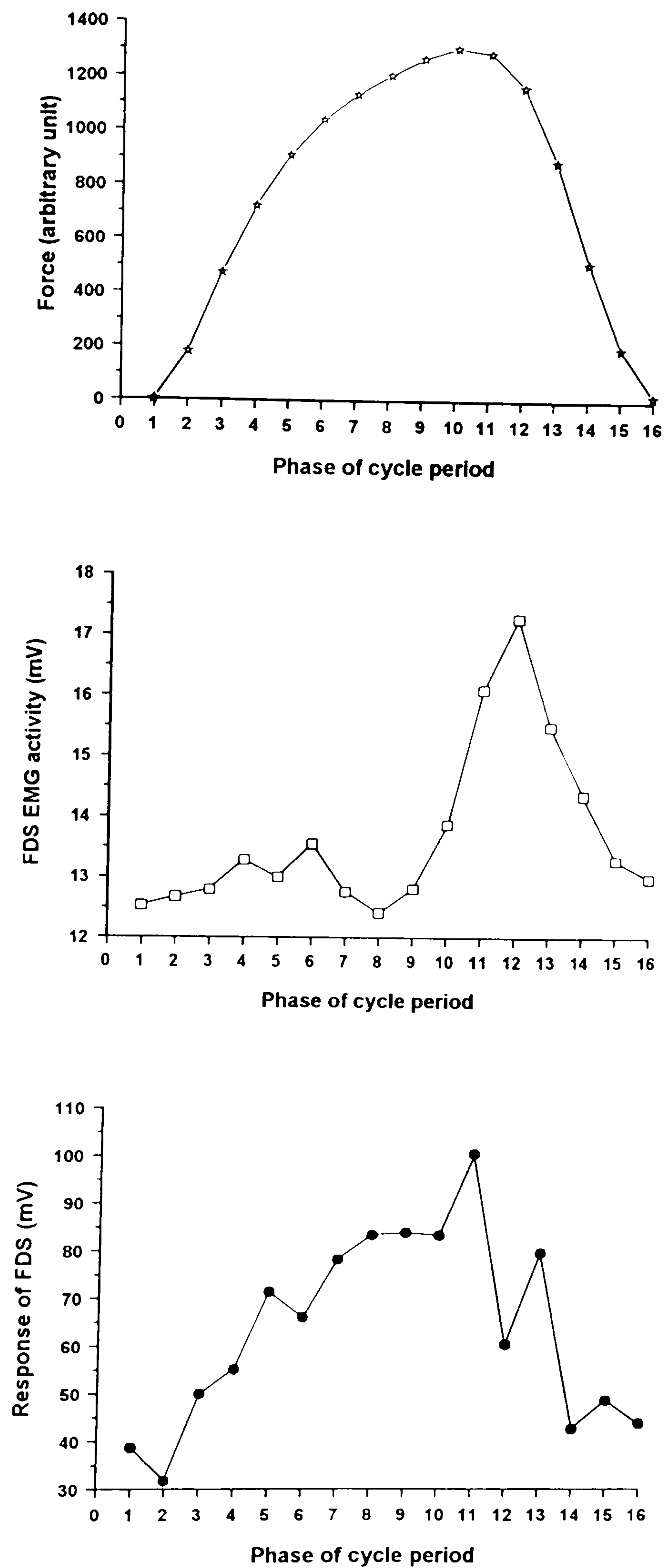
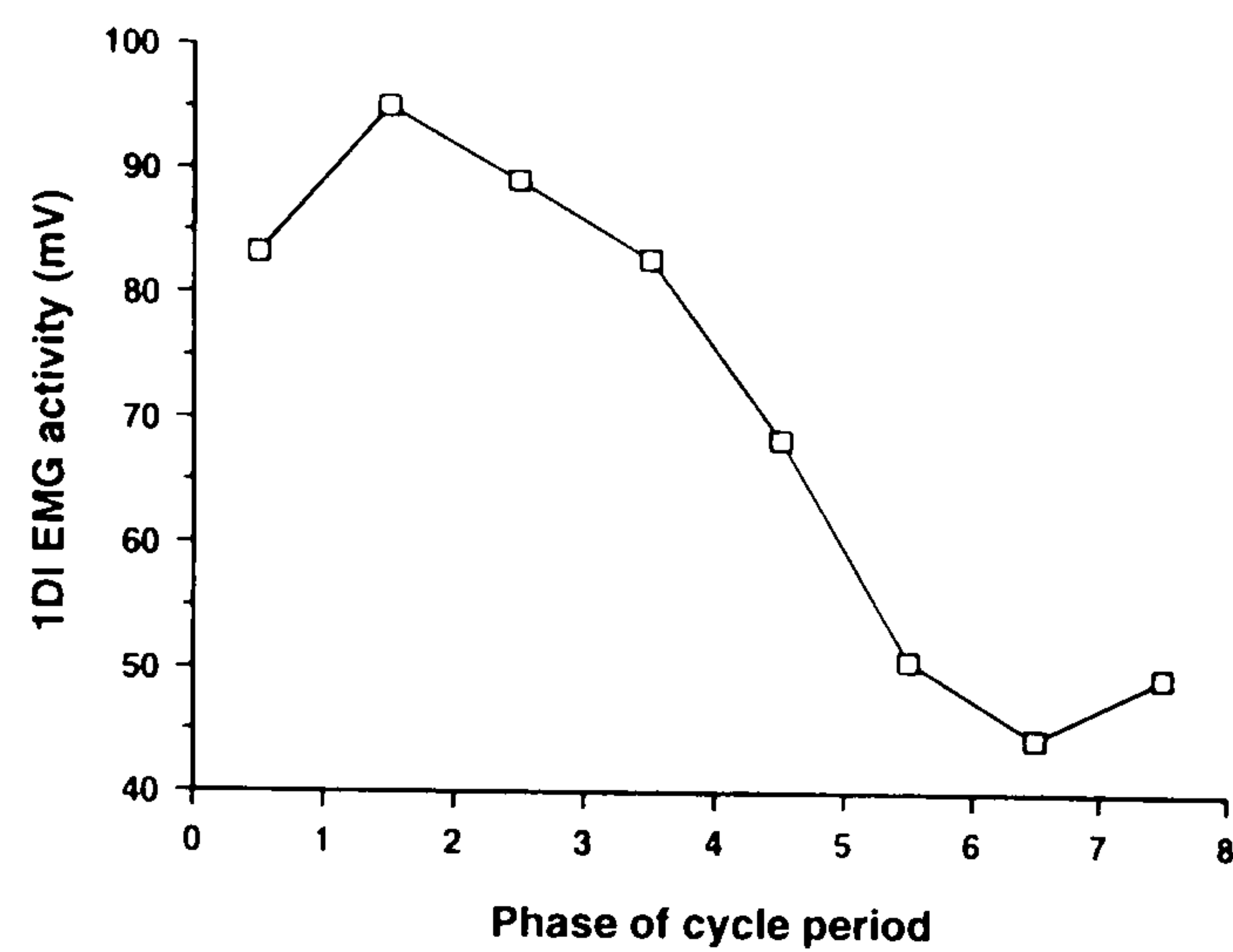


Figure 5.9. Variation of force, EMG activity and reflex responses of FDS during the pen-tip task for one subject. *Top:* Averaged force trace. *Middle:* Mean background EMG activity in FDS over 30 unperturbed cycles. *Bottom:* Reflex FDS responses to all stimuli occurring in each of 16 equal phases.

Subject 1



Subject 2

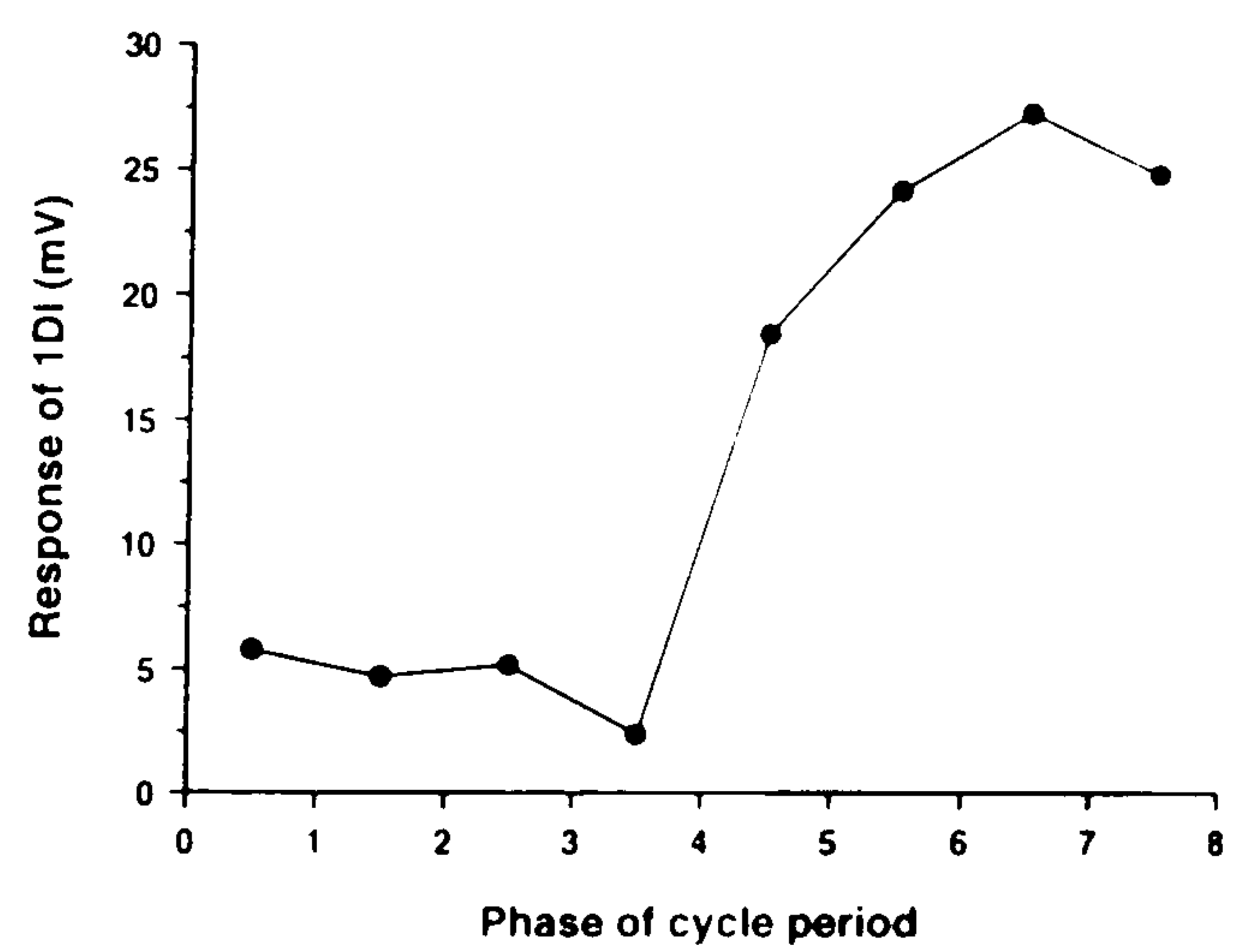
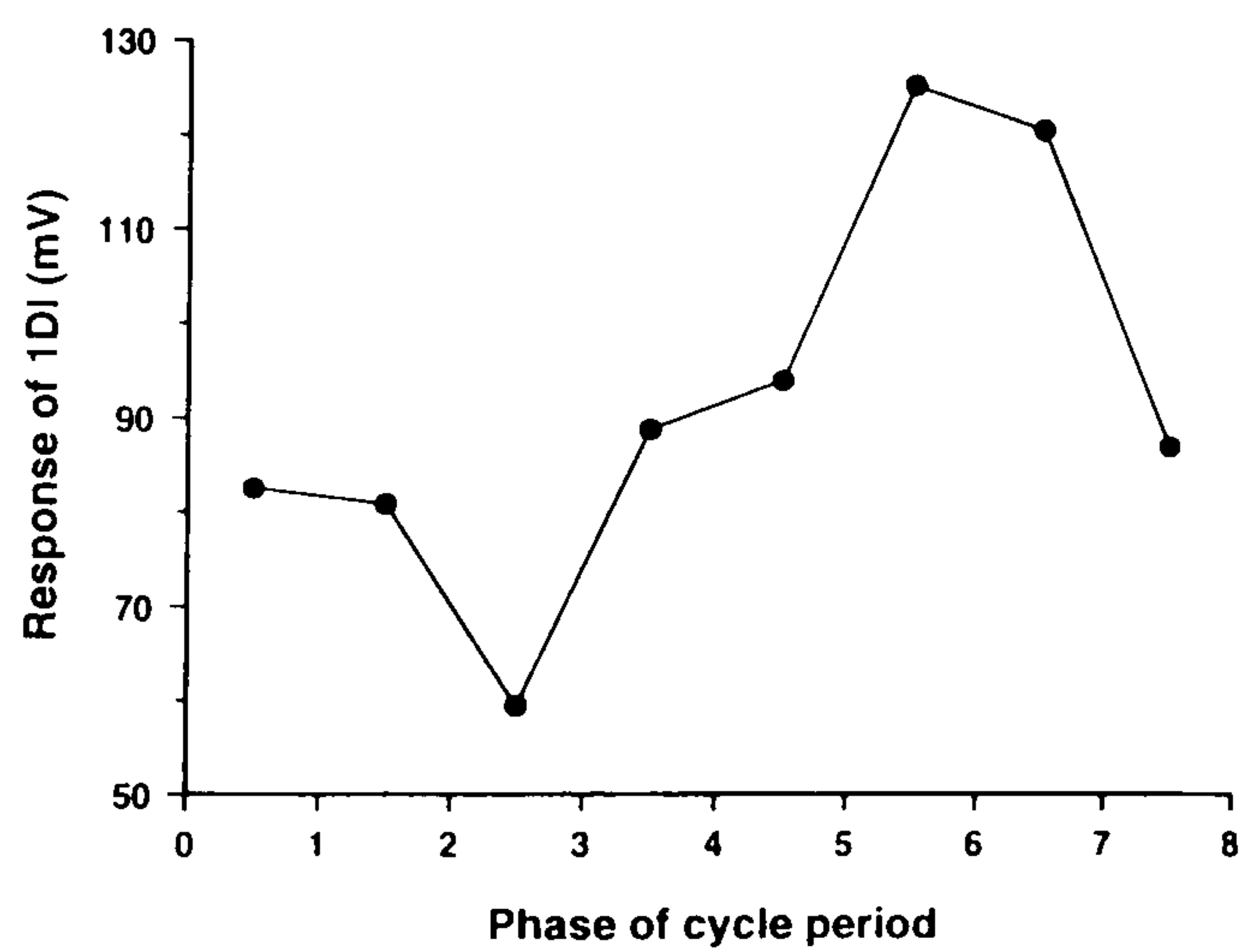
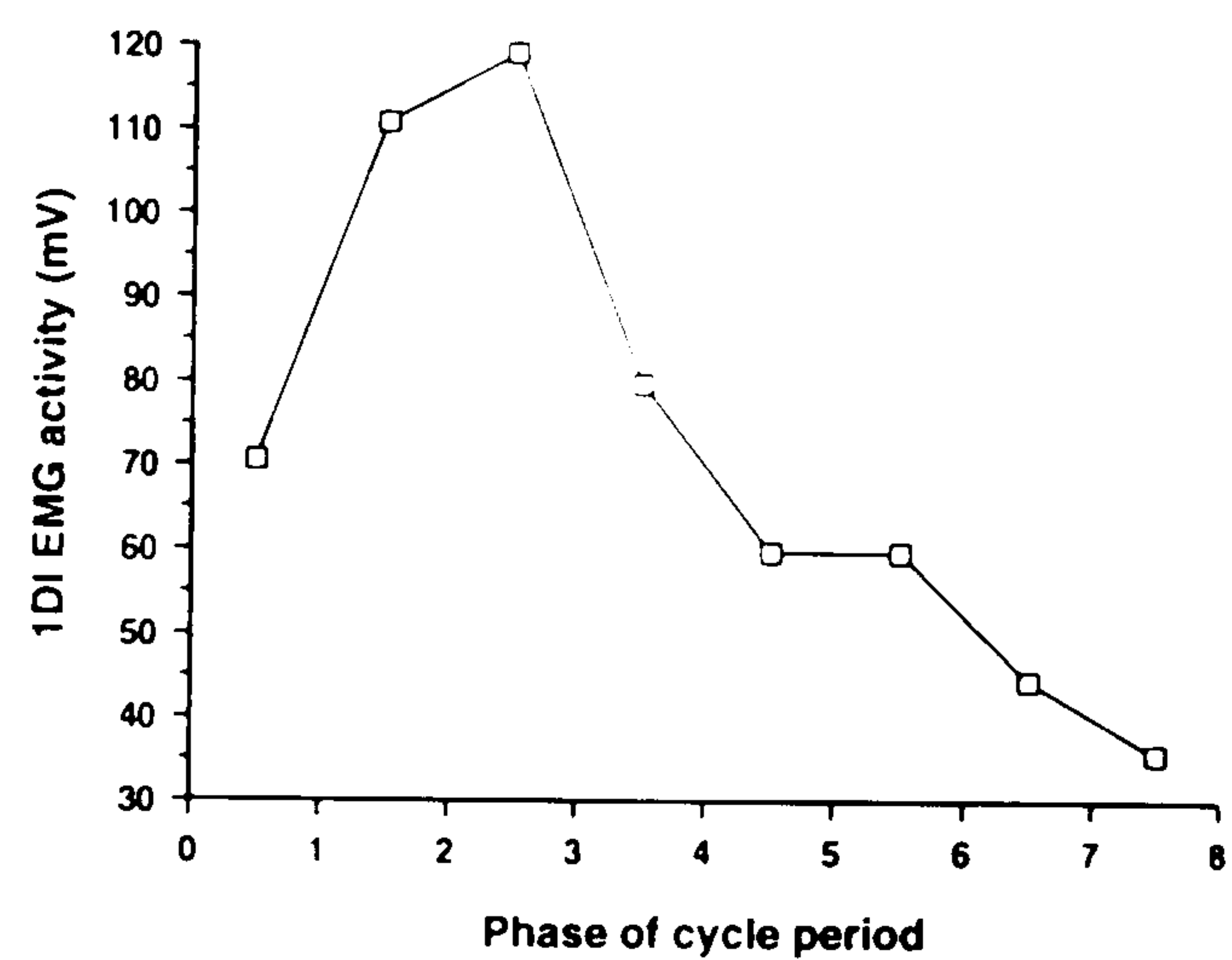
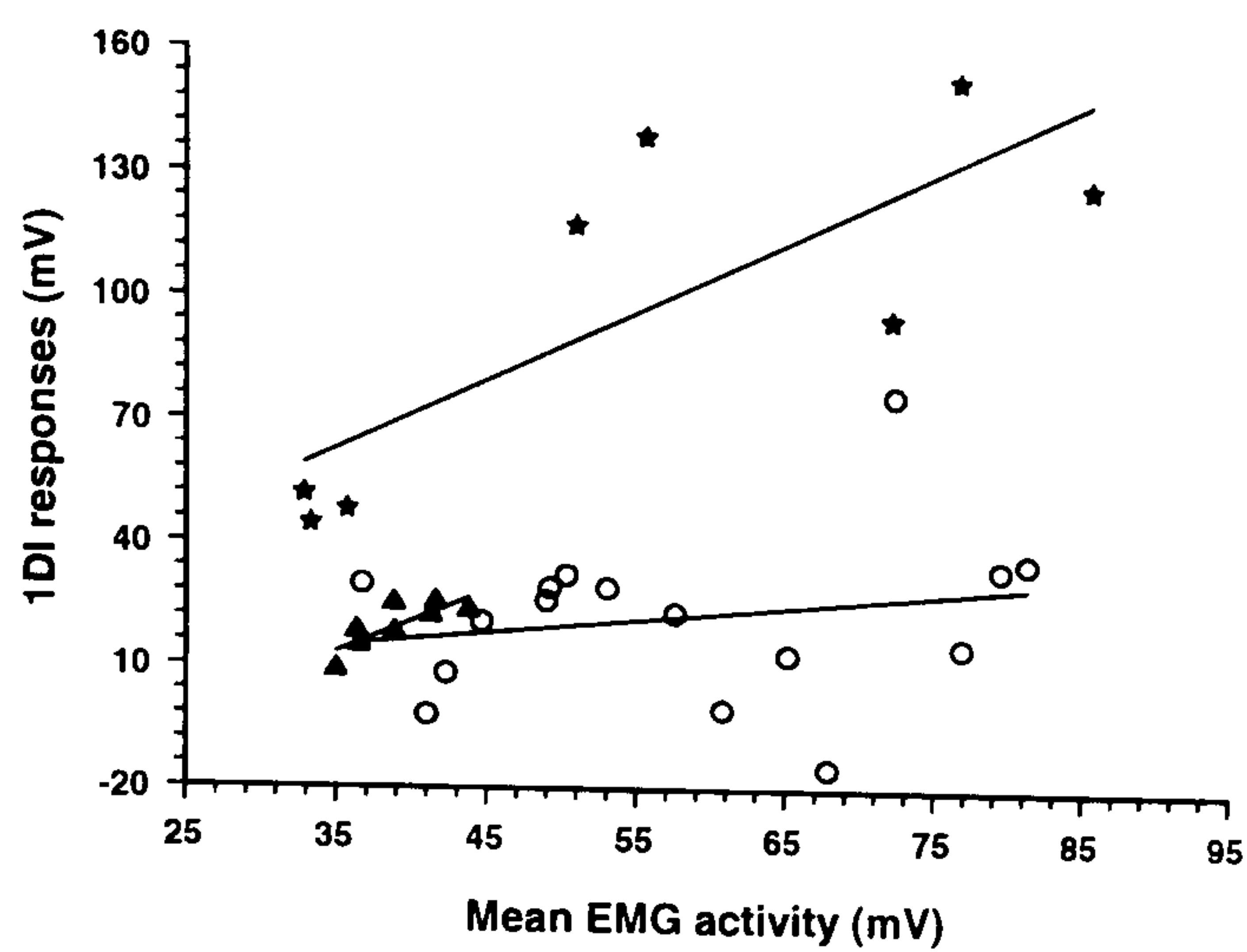


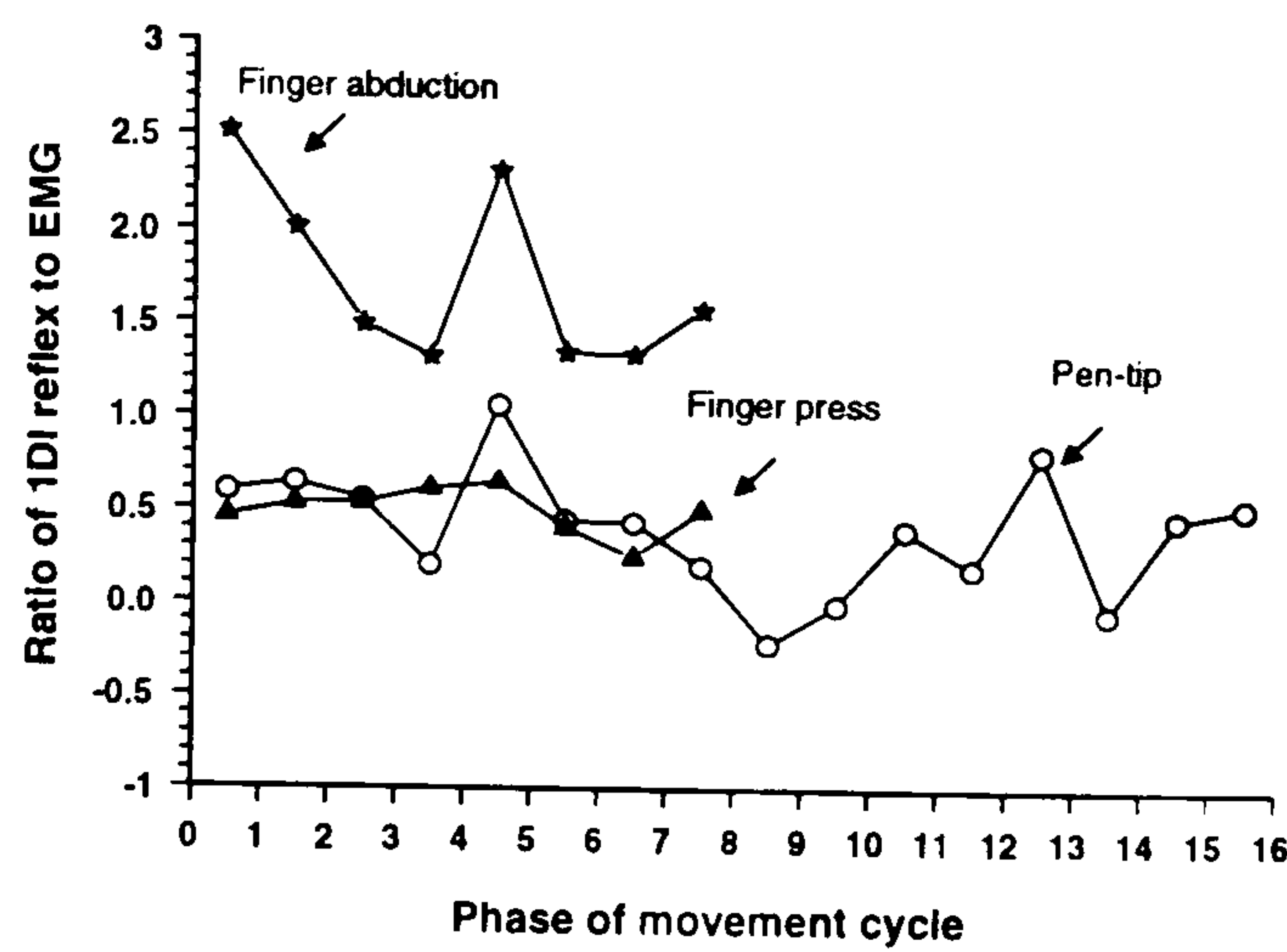
Figure 5.10. EMG activity and reflex responses of 1DI plotted as a function of the cycle phase during the ‘finger abduction/adduction’ task for two subjects.

Subject 1

A

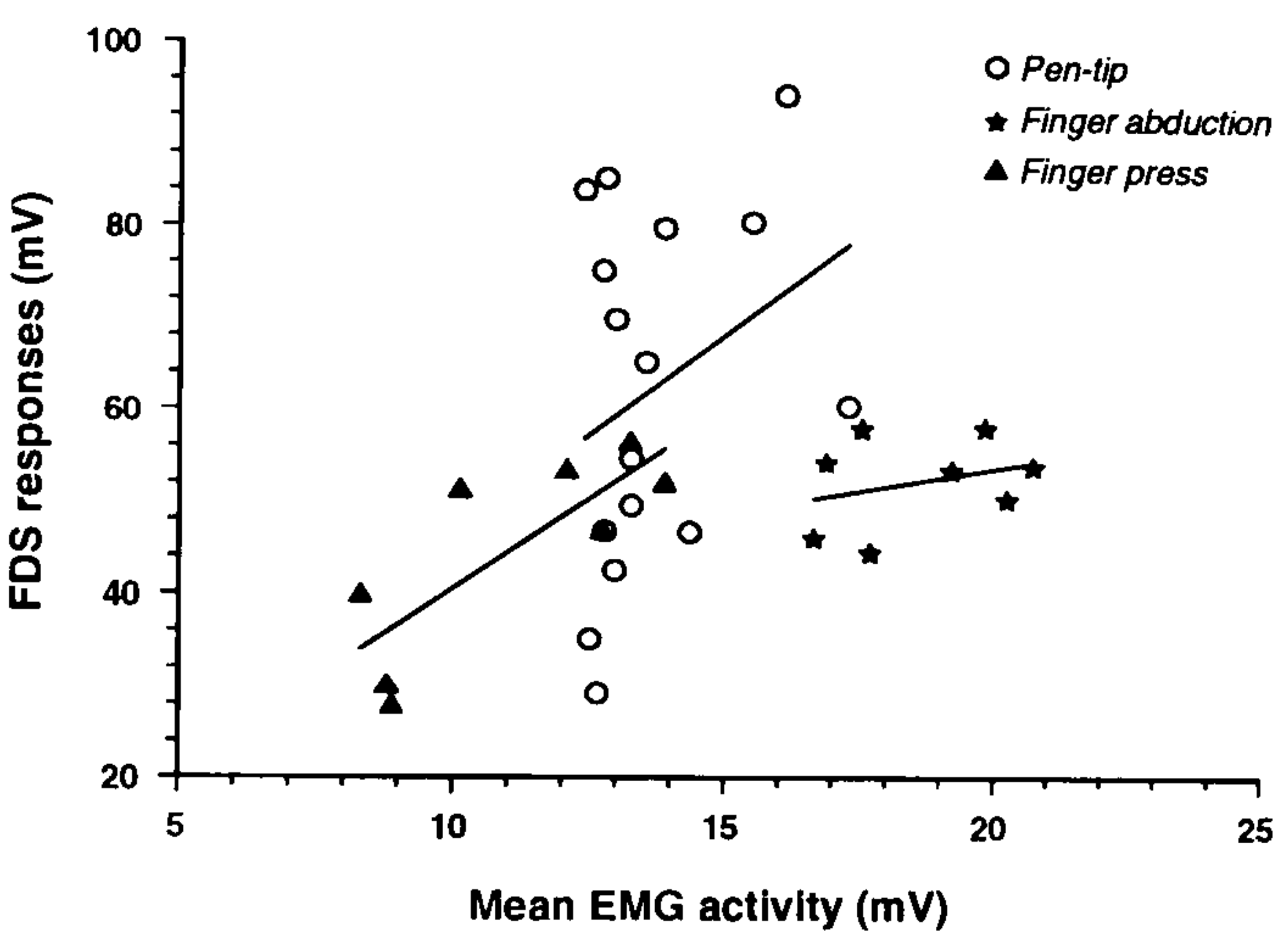


B



Subject 2

C



D

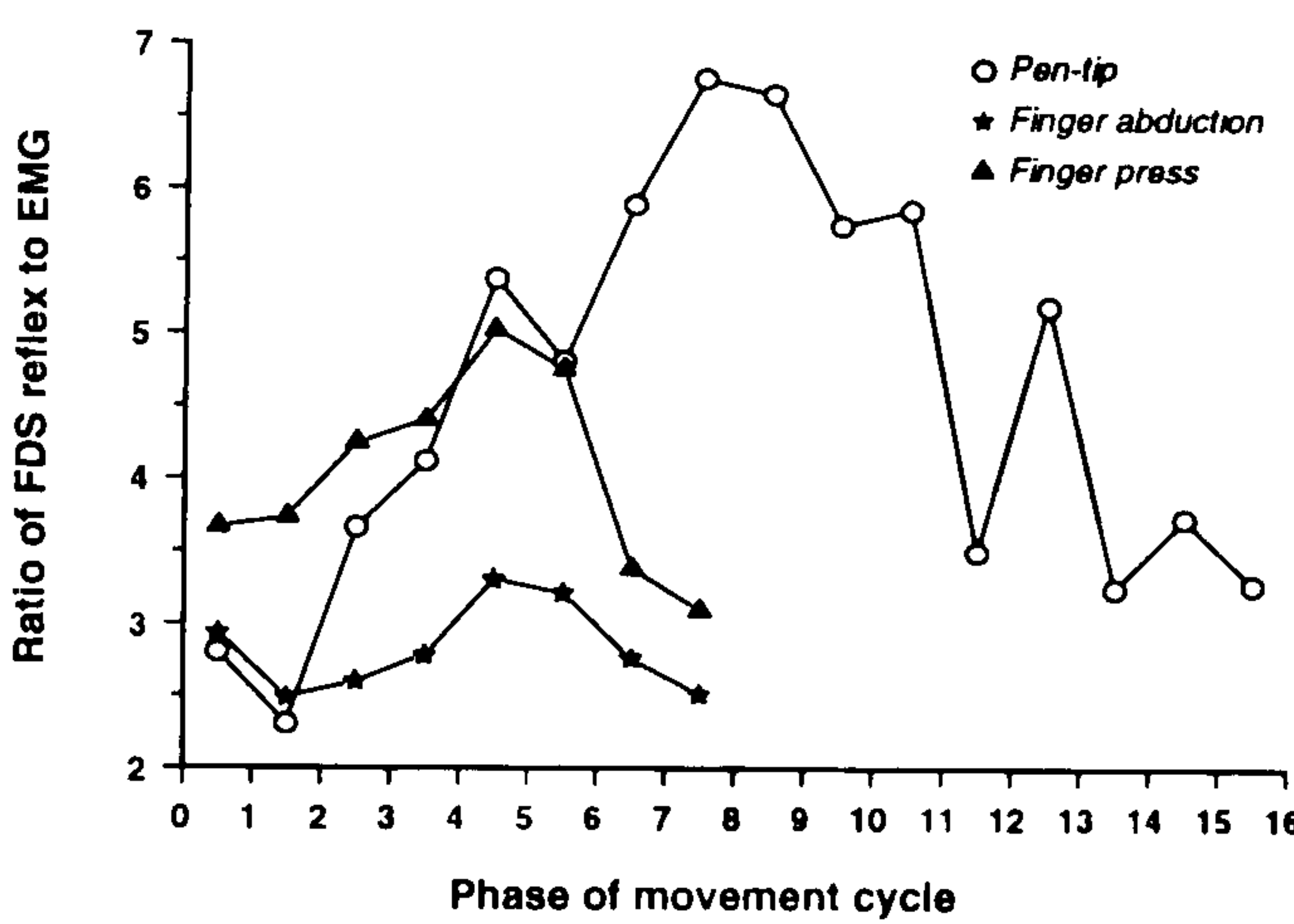
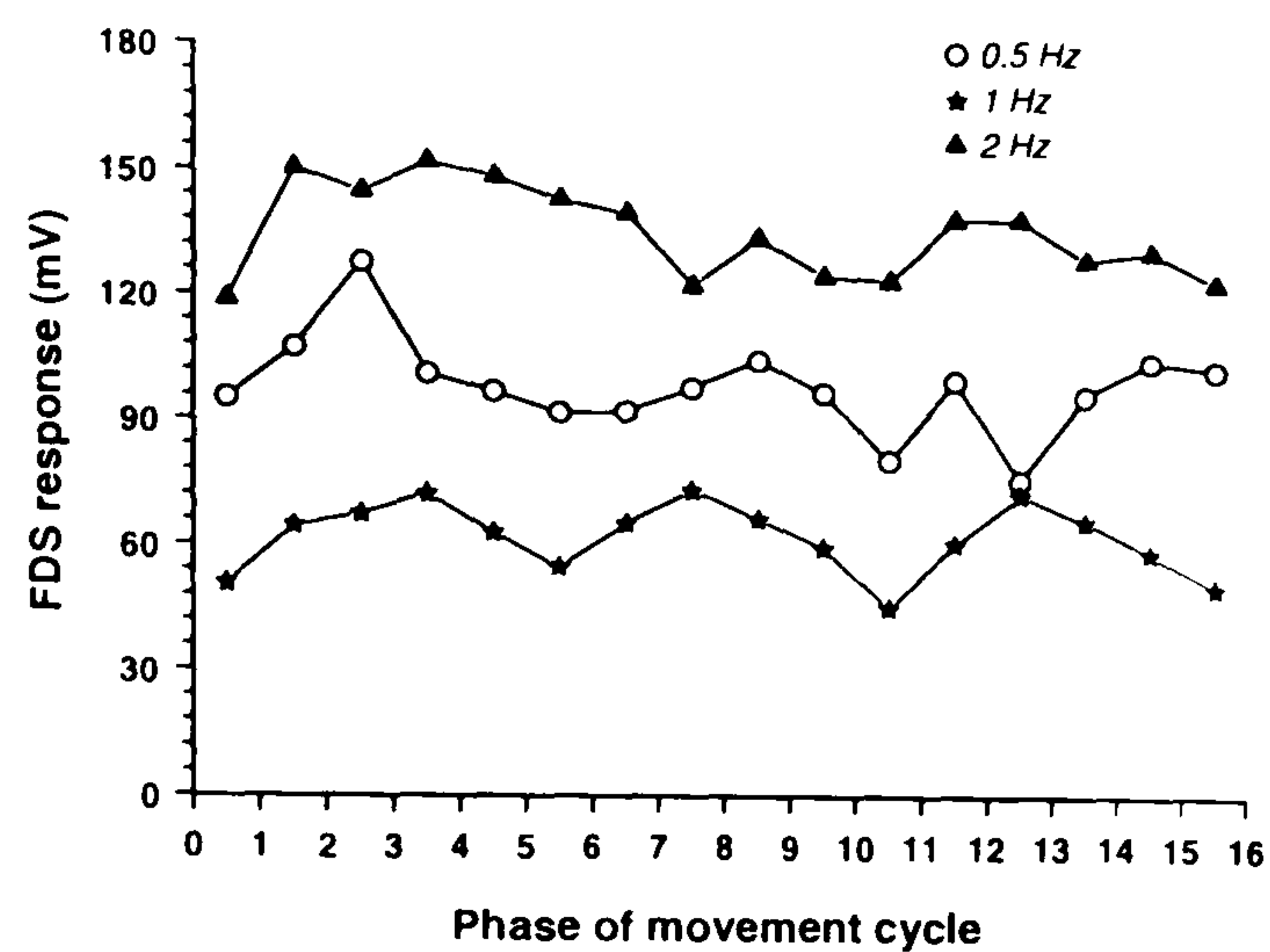


Figure 5.11. Diagrams showing the relationship between the reflex response and the mean EMG background level of 1DI, FDS during three tasks for two subjects. A, C: Reflex response vs mean EMG background activity. B, D: ratio of reflex response to mean EMG activity in the same phase. The slopes of regression lines are 0.324 in ‘pen-tip’ task (circle), 1.696 in ‘finger abduction’ (star), 1.516 in ‘finger press’ (triangle) for 1DI, and 4.382 (circle), 1.009 (star), 3.916 (triangle) in the same task order for FDS, respectively.

A



B

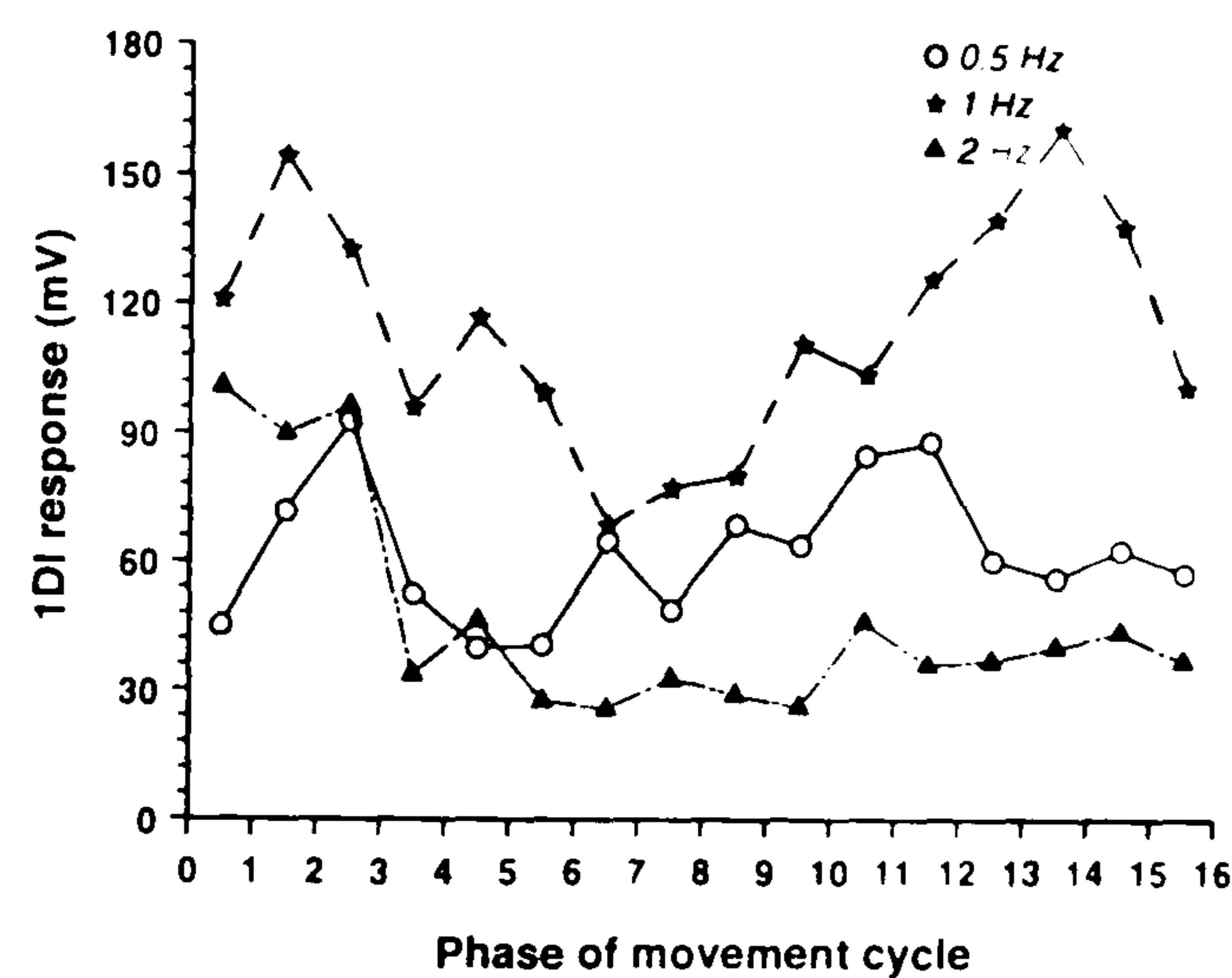


Figure 5.12. Reflex modulation of FDS (A) and 1DI (B) during a pen-tip task performed at three different frequencies: 0.5 Hz, 1 Hz and 2 Hz for one subject.

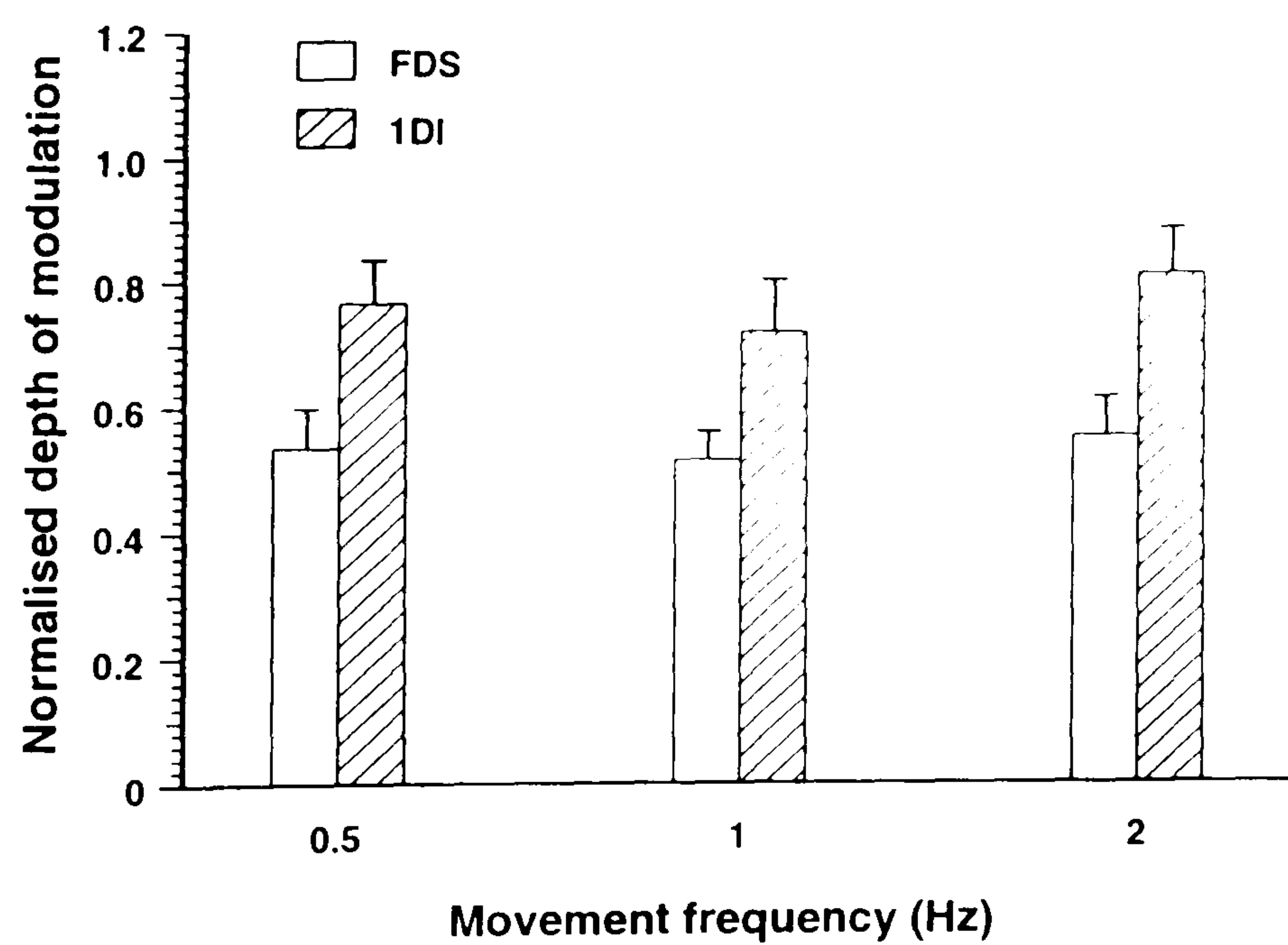


Figure 5.13. Normalised depth of reflex modulation of FDS and 1DI during a pen-tip task performed at three frequencies: 0.5, 1 and 2 Hz expressed as mean + s.e.m. across 10 subjects.

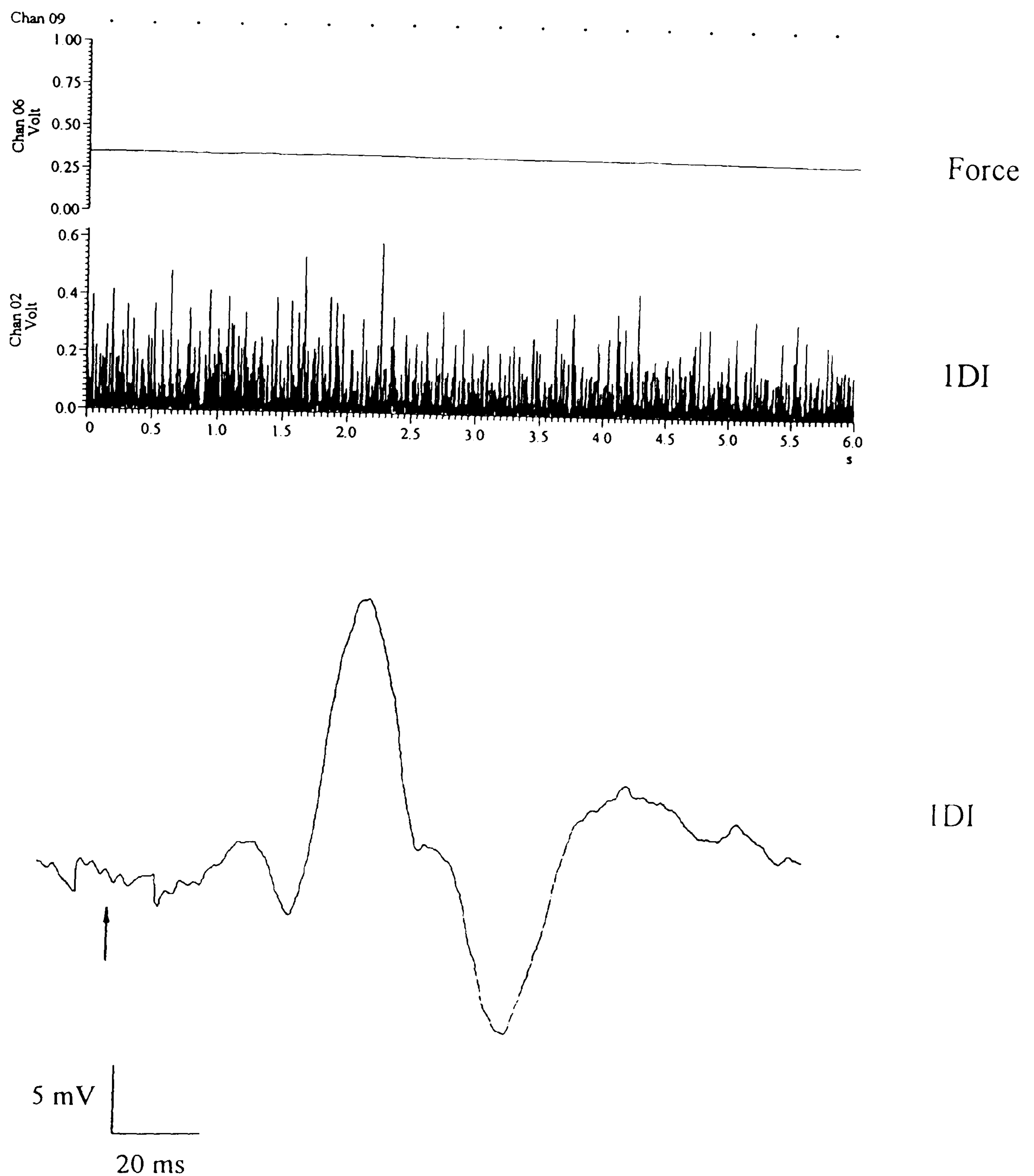


Figure 5.14. Diagrams of EMG recording and cutaneomuscular response of 1DI muscle during steady abduction of the index finger in one subject. *Top:* rectified EMG recording (Channel 2) and sustained force trace (Channel 6) at 25% MVC level; Channel 9 indicates the stimulus timing. *Bottom:* averaged 1DI response over 360 stimuli.

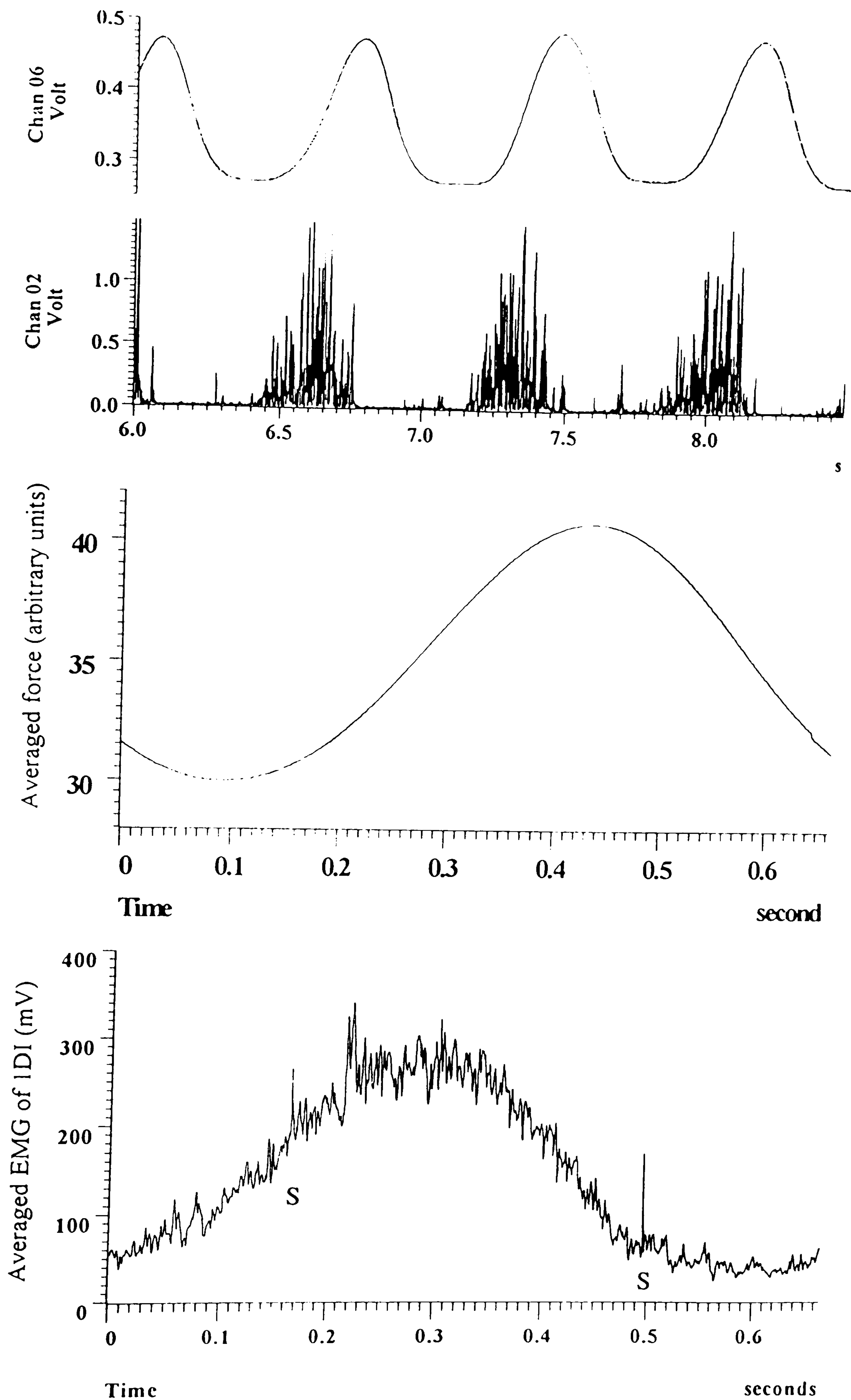


Figure 5.15. EMG and force recordings during rhythmic index finger abduction performed at 1.5 Hz with electrical stimulation applied at the index finger PIP joint at 3 Hz. *Top:* Raw EMG recording of 1DI (Channel 2) and force trace (Channel 6). *Middle:* Averaged force trace within one full cycle. *Bottom:* Averaged cutaneomuscular reflex response shown at two phases of the cyclic finger abduction/adduction. S indicates the timing of the stimulus in each phase.

5.4 DISCUSSION

Determinants of reflex modulation during dynamic finger movements

The findings presented in this study show that the stretch reflex elicited in intrinsic and extrinsic hand muscles is strongly modulated in gain with respect to both phase and task during rhythmic finger manipulations. The dependency of modulation of the reflex gain on the phase within a cyclical manual task was referred to as “phase-dependent”, and the different reflex gain achieved under different finger manipulative conditions will be referred to as “task-dependent”. As clearly shown in Figures 5.6 - 5.9, the modulation patterns of the reflex gain are highly dependent on the phase of the movement cycle in each of the ‘finger abduction/adduction’ and ‘pen-tip’ tasks. These reflexes are modulated to adapt motor programs to match the changing conditions. Suppose that a stimulus occurred during the abduction phase of the ‘finger abduction/adduction’ task. In order to continue index finger abduction, the finger has to overcome the interruption from mechanical perturbation. The stretch reflex elicited in 1DI at the moment is most desirable to compensate the act. During the adduction phase, the 1DI muscle ceases to react to any stimuli as a stretch reflex would now be inappropriate. As such, the FDS response compensated in an analogous way in achieving the successful ‘pen-tip’ and ‘finger press’ manipulations.

Similar patterns of H-reflex modulation have been previously reported in leg muscles during locomotion, such as walking and running (Capaday & Stein, 1986, 1987; Dietz, Faist & Pierrot-Deseilligny, 1990; Edamura, Yang & Stein, 1991). It was found that the H-reflex was strongly modulated in the human soleus muscle as a function of the time. The reflex increased progressively during the stance phase of the step cycle and reached its peak value in the latter half of the stance phase. This large reflex was most desirable to assist with the propulsive phase. The reflex was absent during the swing phase of the step cycle in order to counteract with the ankle flexion to avoid dragging the toe on the ground. The parallel increase in the reflex and the muscle activity during the stance phase and the absence of a reflex during swing phase are

closely matched to the functional requirements of locomotion. Is this modulation automatically associated with the use of a muscle in a voluntary movement, or can the reflex be tailored specifically to the task? This has been tested previously on the basis of different forms of locomotion, e.g. walking and running, as well as standing quietly at varying contraction levels (Capaday & Stein, 1987; Stein & Capaday, 1988). The same pattern is observed in running as well as in walking. But, there exists a difference in slope between walking and running. The slope for running is smaller than for walking.

A neural mechanism was proposed to account for the phase-dependent modulation in human locomotion (Stein & Capaday, 1988). It has been suggested that both presynaptic and postsynaptic inhibition onto α -motoneurons could change the H-reflex gain. Inhibition of transmitter release from the presynaptic terminals of the muscle spindle afferents onto α -motoneurons would reduce the size of the EPSP produced in the motoneurons and hence the probability of discharges from motoneurons in response to the afferent volley (Stein & Capaday, 1988; Stein, 1995). However, postsynaptic inhibition onto α -motoneurons could not only decrease the reflex response, but would also decrease background EMG activity at the same time. An additional source of excitation would have to be added to bring the EMG activity back to its control value. Based upon the observations obtained in their study, they concluded that the H-reflex depends on central neural mechanisms other than the excitation level of the α -motoneurons. Even the shortest latency reflex pathway can be modulated specifically and independently of the prevailing level of motor activity. However, movements of the human hand, especially highly skilled delicate movements, seem to be more subtly controlled by the central and peripheral nervous systems.

The foregoing discussion has shown that the reflex modulation is strongly dependent on the phase of the movement cycle. To what extent does this phase-dependent modulation vary with different manual tasks? The difference in slope of the regression line fitted to the relationship between the reflex response amplitude and the mean level of background EMG, in the three tasks for muscles 1DI and FDS (Figure

5.11A & C), indicated that the reflex sensitivity varied with the tasks performed, and the muscles being investigated. The slope of 1DI was highest in the ‘finger abduction/adduction’ task, whereas the slopes of FDS during the ‘pen-tip’ and ‘finger press’ tasks were much higher than during ‘finger abduction/adduction’. The pattern of reflex modulation also differs between tasks for the same muscle, and between muscles in a given task. In Figure 5.11A and C, all slopes in the three tasks of 1DI and FDS show positive values, indicating that the reflex amplitude increased in parallel with the background EMG activity level. The degree of the increase differed with the nature of the manipulative task. This phenomenon could be interpreted as resulting from “automatic gain compensation” (Marsden, Merton & Morton, 1972, 1976; Matthews, 1986). The human stretch reflex is well known to show automatic gain compensation; in other words, the EMG response elicited by a perturbation increases progressively with the background level of voluntary contraction, and so remains an approximately constant proportion of the pre-existing level. The functional importance of this pattern was first emphasised by Marsden, Merton & Morton (1972, 1976), who analysed such behaviour on interfering with the movement of the thumb and noted that such an automatic gain compensation would ensure that reflexes remained appropriate to the delicacy or otherwise of the task in hand, as well as compensating for fatigue. Automatic compensation of gain reflects the excitation level of the motoneurone pool.

On the other hand, in comparing the reflex gain between different manipulations in the present study, the reflex amplitude of 1DI during the ‘finger abduction/adduction’ task is higher than the other two tasks, whilst the reflex gain in FDS during ‘pen-tip’ and ‘finger press’ are higher than during finger abduction. The phenomenon was also reflected in the ratio of the reflex to the mean EMG background (Figure 5.11 B & D). If automatic gain compensation was the only determinant of the reflex gain, one would expect reflex amplitude with the same background contraction level to be identical, irrespective of the form of the movement. However, this was not the case in either 1DI or FDS. This observation indicated that automatic gain compensation is not the only factor that determines the modulation of reflex gain. In association with muscle

function, 1DI mainly acts as an index finger abductor although it also acts synergistically in flexing the proximal phalanx. Thus, 1DI plays a more important role in performing the 'finger abduction/adduction' task than the 'pen-tip' and 'finger press' manoeuvres, which were mainly achieved by finger flexors including muscle FDS.

Another mechanism to account for the task-dependent modulation is the effect of presynaptic/postsynaptic inhibition, as used to explain the phase-dependent modulation at different times of the movement cycle, and the comparable studies on locomotory rhythms, which showed that the soleus H-reflex sensitivity for walking is higher than that for running (Capaday & Stein, 1987). In a more recent study which investigated the most important factor in setting this slope, it was reported that the primary determinant of the slope was found to be the form of locomotion (Edamura, Yang & Stein, 1991). The form of locomotion dominates the gain of the soleus H-reflex. Presynaptic inhibition would reduce the size of the reflex only whereas postsynaptic inhibition can change both reflex gain and EMG activity level simultaneously. As described in the results of the present study, a negative correlation was observed between the reflex amplitude and the background activity in some cases. Apart from presynaptic inhibition, presynaptic excitation may also be involved in the control of the modulation pattern. The excitation could act onto motoneurons via Ia spindle afferents. The summation of each individual effect regulates the reflex gain in order to obtain the optimal motor performance.

More recently, Dietz, Discher and Trippel (1994) proposed a neural mechanism to explain the task-dependent modulation of short- and long-latency EMG responses. They investigated the function of compensatory mechanisms in upper arm muscles under two motor conditions: control of elbow position and control of joint torque. The long-latency EMG response M2 was modulated by the two tasks. The significant differences in the behaviour of the M2 component between position- and torque-control were observed from the shape of the EMG responses. It was proposed that the task-dependent modulation of the M2 component may be because the muscle spindles

responded in a more dynamic fashion during a position-controlling task than during a torque-controlling task. Such a change could be achieved by the appropriate central regulation of gamma-motoneurone activity. Alternatively, different proprioceptors may be activated by the two tasks.

Our results showed that the modulation patterns of the stretch reflexes, in some extent, relied on the excitation level of motoneurone pool as defined by the 'automatic gain compensation'. However, the modulation patterns also displayed to be partly independent of the α -motoneurons excitation level. It might be therefore concluded that the stretch reflexes evoked during dynamic finger manipulations akin to handwriting were modulated by the interactions between the central and peripheral neural mechanisms, reflecting the specific motor strategies adapted to the optimal performance of skilled, delicate hand movements.

Methodological consideration

As described in Chapter 2: Materials and Methods, the vibrator used to apply mechanical displacement in this study was run open-loop, without servo control. If the movement was performed under steady contractile conditions, one would expect the strength of the stimulus from the prodder to be constant. However, the three manipulatory tasks were performed under dynamic conditions. The pseudorandom stimuli were applied at various phases of the movement cycle. The resultant force, which was measured as the summation of the force generated by the index finger and the prodder, changed at different phases. Therefore, the stimulus strength, as represented by pulse amplitude, varied with the phase of the cycle. The influence of the stimulus strength on the size of the stretch reflex was examined during the performance of the isometric constant contraction at different levels in the course of this study. The stronger the muscle contracted, the lower was the stimulus strength which resulted from the index finger and the prodder. The results from the examination show that the size of the reflex increased with the strength (i.e. amplitude) of the stimulus applied at the index

finger. This effect may decrease the degree of the phase-dependent modulation. It could also result in the inconsistent modulation pattern between individual subjects.

In order to standardise the conditions in all subjects, the same percentage of MVC contraction level between two force limits was set being aimed at by each subject during cyclical movements. The force produced by the index finger via the force pen, was shown on the oscilloscope to monitor the voluntary contraction level during the ‘pen-tip’ task. In order to minimise the effect induced by the open-loop vibrator, each subject was asked to maintain the pressure on the prodder as constant as possible. The subject was supposed to maintain two force traces at the desired levels at the same time. The ‘pen-tip’ task, therefore, became relatively difficult to perform. During the ‘finger abduction’ and ‘finger press’ tasks, although it was easier for subjects to aim to follow just a single force trace in series with the prodder, the influence of the stimulus strength must contribute significantly to the size of the reflex gain. The observation that a negative correlation appeared between the reflex gain and the mean background EMG activity level in several cases may be related to this negative effect (Figure 5.10). The reflex gain varied inversely with the pre-existing EMG activity level. Therefore, a newly designed vibrator run by closed-loop, servo control appears to be necessary for further investigation, in particular under dynamic conditions in which the muscles are activated phasically.

Short- and long-latency EMG reflex components in distal and proximal hand muscles during the static ‘pen-tip’ task

In the results part, it was shown that the latencies of the reflex responses elicited in two distal hand muscles FPB and 1DI were significantly longer than that in two proximal forearm muscles EPB and FDS. The latency of the M1 component is comparable with that of corresponding monosynaptic tendon jerk reflexes of leg muscles. The distal hand muscles have longer reflex latencies than the proximal hand muscles as their conduction distances are longer. In addition, the long-latency component was also elicited in distal hand muscles in most subjects, whereas only the

short-latency reflex component was evoked in the proximal forearm muscles. This later activity following the M1 component is more difficult to assess. The study of the long-latency component of the stretch reflex has been especially attracting many neurophysiologists. It started some 40 years ago when Hammond (1954) set out to measure the mechanical effectiveness of the human stretch reflex in resisting a disturbance applied during a steady voluntary contraction. He did not get very far with this, but he introduced two key concepts which continue to dominate our attention. First, he sub-divided the human stretch reflex into early and late components and initiated the debate into their respective mechanisms. Second, he considered that the magnitude of the later component could be crucially modulated by the neural 'set' of the subject.

Experimental work suggests that the long-latency component of the stretch reflex can be mediated by more than one reflex mechanism. These different reflex mechanisms may contribute in varying degrees to the long latency reflex, depending on the muscles being studied, on the parameters of stretch and on the instructions given to the subject. There is a possible explanation for the observation obtained in our study that, during the constant 'pen-tip' task, the long-latency stretch reflex was evoked only in distal hand muscles FPB and 1DI, but not in proximal muscles EPB and FDS. The long-latency reflexes elicited in the intrinsic hand muscles rely more heavily on the low threshold stretch receptors than the more proximal forearm muscles. This was supported by a number of previous investigations. Phillips (1969) originally suggested that in primates the transcortically mediated long-latency reflex is predominantly active in small hand muscles, as inferred from the heavy monosynaptic corticospinal projection to their motor nuclei in the spinal cord. However, this notion lacks experimental support. There are some experimental hints pointing to such a difference in reflex control. Angular dorsal displacement of the human wrist joint readily evokes short- and long-latency reflexes of the activated wrist flexors, denoted M1, M2 and M3 (Lee & Tatton, 1975). When the duration of the ramp phase of the displacement is shortened step by step, the long-latency reflex disappears at stretch amplitudes at which the short-latency reflex is still unaffected (Lee & Tatton, 1982). The opposite result has been obtained in

the human 1DI muscle. Here small angular displacements elicit long-latency reflex responses with lower threshold than short-latency responses (Noth *et al.* 1991).

Another line of evidence supports the latter view as well. Small amplitude vibration of proximal arm muscles evokes sizeable short-latency reflexes, but no or only weakly expressed long-latency reflexes (Matthews, 1984). On the other hand, ramp stretches of these muscles readily elicit long-latency reflex activity. It has been tested by Noth *et al.* (1991) that Matthews' finding is also valid for intrinsic hand muscles. Vibration was applied to the index finger of healthy humans during a steady voluntary flexion task under three different conditions: (1) imposed small transient extension of the index finger; (2) train of vibration applied to the index finger; and (3) ramp-and-hold stretch. The average of the integrated EMG activity during the period of the long-latency reflex was not significantly different under the three conditions. Even complete anaesthesia of the index finger including the radial aspect of the hand did not abolish the long-latency reflex elicited either by vibration or small transient stretches. The conclusion can be drawn therefore that the first stroke of a vibration elicits the long-latency reflex in intrinsic hand muscles by the excitation of primary muscle spindle endings (Noth & Schwarz, 1991). In a recent study by Matthews (1994), the stretch reflexes of a distal muscle, the abductor digiti minimi, and a proximal muscle, the biceps brachii, were compared using small-amplitude sinusoidal stretching at 10-50 Hz. Biceps brachii was found to be controlled by short-latency reflex pathways and the abductor digiti minimi by long-latency pathways.

Results of the present study show that short-latency stretch reflexes (M1) are displayed in both distal hand and proximal forearm muscles under study, and long-latency stretch reflexes (M2) are observed in distal hand muscles only. These observations reinforce the view described above. The transcortical loop via low threshold muscle and skin afferents dominates in intrinsic hand muscles. Further investigation could be made on other distal and proximal muscles during the same form of movement or the same group of muscles under different conditions.

Influence of the frequency or speed of movement on reflex modulation during the rhythmic ‘pen-tip’ task

In this study, the effect of the dynamic movement speed or repetition frequency on the reflex modulation pattern was investigated in one of the rhythmic finger manipulations: the ‘pen-tip’ task. The results showed that the frequency of rhythmic movement had little effect on the depth of reflex modulation elicited by mechanical stimulation during the ‘pen-tip’ manipulation. A primary difference between the three frequencies used (0.5, 1, 2 Hz) was that the time spent on each movement cycle was shorter in the faster movement than the slower movement. However, the proportion of the time spent on the dynamic phase versus the static phase was equal under different conditions. The subject was asked to aim at the same force level while performing each task, so the mean muscle contraction level was kept the same. Although the reflex gain is not tightly dependent on the background activation level, pre-existing muscle contraction level does have some effect on the reflex gain, as defined by the ‘automatic gain compensation’. This effect was clearly shown in some examples from this study where the reflex gain increased roughly in parallel with the background EMG activity level (Figures 5.8 and 5.9). Since subjects aimed at the same muscle contraction levels under different paced movements, therefore, the same pattern of reflex modulation was expected. Previously, Edamura, Yang and Stein (1991) investigated the factors that determine the reflex gain of the human H-reflex in locomotion. They found that the gain of soleus H-reflex was largely determined by the form of locomotion. Substantial differences in the reflex gain between walking and running could not be explained by movement speed. In the present study, the form of the task under the three movement speeds is essentially the same.

Modulation of cutaneomuscular reflex of 1DI during repetitive ‘finger abduction/adduction’ task

Results obtained under steady state showed great similarities to those of previous studies (Caccia *et al.* 1973; Jenner & Stephens, 1982; Evans, Harrison & Stephens, 1989). In those studies, it was generally shown that electrical stimulation of the digital

nerve of the index finger evoked a remarkably clear reflex response in the activated 1DI muscle during steady voluntary contraction in a variety of tasks. Typically, this reflex response comprises three easily identifiable components, reflecting a short-latency increase in EMG (E1), then a decrease (I1), followed by a further increase (E2). Under dynamic conditions, an identifiable reflex response was evoked in the abduction phase in which 1DI was contracting, whereas no response was elicited in the adduction phase in which 1DI was relaxed, as illustrated in Figure 5.15. The reflex evoked in the abduction phase would assist in the performance of the movement, while a lack of reflex response in the adduction phase would also be appropriate for the execution of the movement. These results thus again show the role of phase-dependent reflex response modulation in the control of rhythmic movement. Unfortunately, no obvious reflex response was elicited in other tested subjects. A further study is needed to investigate a larger number of subjects.

CHAPTER 6

ELECTROMYOGRAPHIC STUDIES IN WRITER'S CRAMP

6.1 Introduction

As part of the work in this study, writer's cramp has been briefly introduced in Chapter 1, 'General Introduction'. This Chapter will particularly centre on the electromyographic patterns of hand muscles in writer's cramp. Writer's cramp or scrivener's palsy has been recognised and discussed for at least a century. Compared with the late 1800s, the incidence of writer's cramp today has decreased due to the advent of typewriters and computers. Because of the request of enormous office staff, writer's cramp appeared to have been widespread in the late Victorian era. In the English literature, Poore (1878, 1897) described his examinations of many hundreds of patients with writer's cramp. Solly, a Senior Surgeon at St. Thomas' Hospital, wrote in a clinical lecture on 'Scriveners' palsy or paralysis of writers' in 1864. In Victorian times, the frequency of the disorder was much higher in men than in woman. Today, it affects both female and male equally. The peak incidence of writer's cramp is in the third, fourth and fifth decades (Sheehy & Marsden, 1982; Sheehy, Rothwell & Marsden, 1988). It is estimated that there are at least 4000 people suffering writer's cramp in the UK. This is probably an underestimate, as it seems in general that the condition is either not recognised or many with this condition do not bother to seek medical help.

Although writer's cramp was known more than a century ago, its cause and pathophysiology remain a mystery. Whether it is a physical disorder or a true focal dystonia continues to be debated. Originally, writer's cramp was considered as psychic rather than motor pathology because the use of the descriptive term 'professional neuroses', coupled subsequently with fashion in psychiatry, led to the mistaken belief. According to Gowers (1888), the first description of writer's cramp appeared in the eighteen thirties. Since that time, most authors have found common ground when describing some clinical features of writer's cramp and other occupational neuroses. Gowers gave a clear description of the features of the disorder. He thought that writer's cramp was likely to be a disorder of the *CNS*, but the site of the involvement was not clear. Subsequently, writer's cramp was labelled as a psychoneurotic disorder or even an

hysterical disorder. More recently, this puzzling condition was viewed as psychosomatic disorder (Crisp & Moldofsky, 1965). Despite the obvious lack of therapeutic response to this, the view that writer's cramp was due to psychoneurotic or psychosomatic illness has been widely accepted, not only in psychiatric publications, but in some neurological texts as well. However, most recent evidence supports the notion that writer's cramp is a focal task-specific dystonia, that is a group of motor disorders characterised by involuntary sustained muscle contractions, causing twisting and repetitive movements or abnormal postures (Sheehy & Marsden, 1982; Marsden & Sheehy, 1990). Examinations on a large number of patients with writer's cramp indicated that stress, depression or trauma appeared to contribute to developing this condition in some cases (Sheehy, Rothwell & Marsden, 1988). In an earlier study, writer's cramp subjects were given a formal psychological assessment and compared with a control population. The results of the formal PSE (present state examination) survey confirmed that writer's cramp sufferers did not show any excess of psychiatric illness compared to a normal population (Sheehy & Marsden, 1982).

Writer's cramp can be classified into three different types. Simple writer's cramp is affected with only the act of writing, not with other manual motor tasks. As soon as they pick up the pen, or write some words for a while, dystonic postures of the hand appear to impede the performance of writing. Dystonic writer's cramp demonstrates difficulties not only with writing but also with other manual tasks, e.g. using eating utensils, applying shaving, cosmetic or even lifting a full cup or glass. Patients with progressive writer's cramp begin with a simple writer's cramp, but later develop dystonic writer's cramp (Sheehy, Rothwell & Marsden, 1988; Marsden & Sheehy, 1990).

A typical writer's cramp may present common clinical features. Abnormal postures of the hands, fingers or wrists often occur on attempting to write. The hand may pronate, with elevation of the elbow, hyperpronation of the forearm. The pen is often held very tightly, with an exaggeration of normal thumb and finger semiflexion

and with hyperextension of the distal interphalangeal joint of the index finger. Some patients exhibit sudden jerks of the hand and arm during writing. This may cause unintended marks of the pen. Tremor and a complaint of fatigue are usually common during attempted writing. The extent of muscle spasm often increases as the patient tries to continue with writing. Pain is a less common feature of writer's cramp whereas tension or discomfort is more commonly felt in the fingers and forearm, or even in the upper arm and shoulder (Sheehy & Marsden, 1982; Marsden & Sheehy, 1990).

Writer's cramp sufferers try various ways to counteract the difficulty with writing. Many with this condition change the mode of holding the pen in attempts to overcome these problems, sometimes holding it vertically between the index and middle fingers, or in a closed fist. Some patients hold the pen with the thumb, middle, ring and little fingers flexed across the palm. Some lift the index finger off the pen and extend it. Some hold the pen between thumb and lateral side of the index finger and twist the hand excessively. Sometimes, the opposite hand is employed to steady the affected limb in order to carry on writing normally. Commonly, they found it much easier to use thick pens or pens with different barrel. This problem does not seem to occur while writing on the blackboard with a piece of chalk. Surprisingly, Gowers (1888) as well as Marsden and Sheehy (1990) reported that individuals whose longhand was impaired did not have any problem with shorthand. It seems to be that this disorder affects the detailed successive action.

Neurophysiological studies on writer's cramp provide additional evidence that writer's cramp is a disorder of motor control. It was Oppenheim (1911) and Foerster (1921) who first noted the excessive co-contraction or co-activation of antagonist muscles and the overflow of contraction into remote muscles that characterise dystonia. Recent electromyography (EMG) investigations have shown that instead of normal alternating contraction of agonist and antagonist muscles, patients with writer's cramp show co-contraction of antagonist muscles (Rothwell *et al.* 1983; Hughes & McLennan, 1985). In particular, this typical co-activation appeared while performing more delicate,

precision tasks, rather than rapid limb movement, as shown in Figure 6.1 by Rothwell *et al.* (1983). As early as in 1954, Reis found by examining 17 subjects with writer's cramp that all the muscles studied showed increased levels of muscle activity on writing, including not only forearm flexors and extensors, but also biceps, triceps, deltoid and trapezius. In addition, patients with writer's cramp present some difficulties in selecting the appropriate muscles to perform the task and unintended muscle contraction into inappropriate muscles.

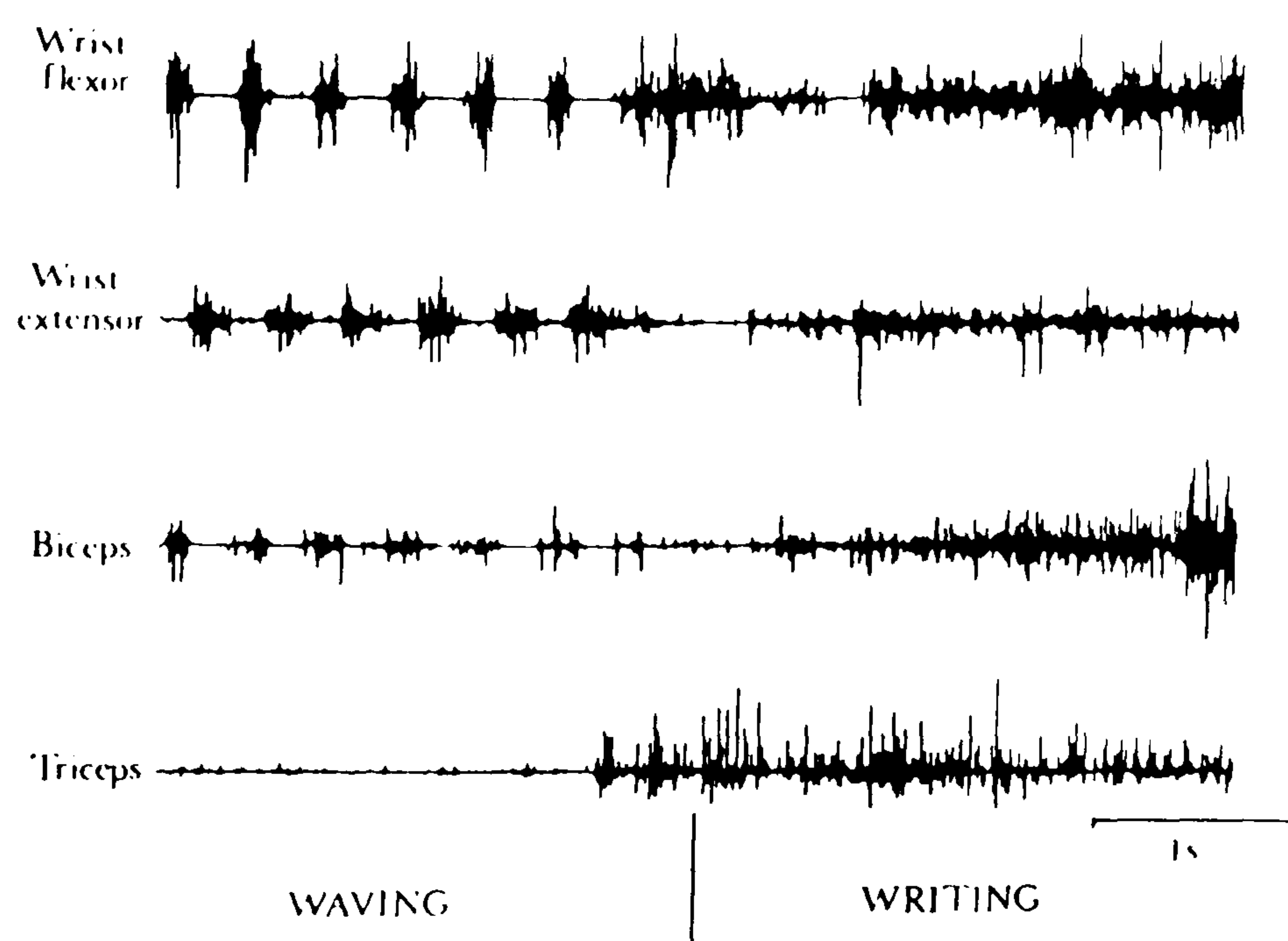


Figure 6.1. Normal reciprocal activation of wrist flexors and extensors during waving (left) and resumption of typical co-contraction when the subject stops to pick up a pen and write his name (right). (From Rothwell *et al.* 1983)

The excessive co-contraction of antagonist muscles in dystonia can be interpreted as a disorder of the normal reciprocal inhibitory mechanism. In normal subjects, activity of a pair of antagonist muscles is controlled by reciprocal inhibition, which is mediated by two different mechanisms. Both of them probably utilise the same spinal Ia inhibitory interneurons, termed as peripheral and central inhibitions. When the agonist muscles receive an excitatory input causing them to contract, the antagonist muscles receive an inhibitory input to prevent muscle contraction. If there is a breakdown in reciprocal inhibitory control, it could lead to the co-contraction of antagonist muscle groups.

Apart from the investigations on the voluntary movements in patients with writer's cramp, the more recent physiological development has contributed to the measurement of reciprocal inhibition in this condition in comparison with normal condition (Rothwell *et al.* 1983; Sheehy, Rothwell & Marsden, 1988; Nakashima *et al.* 1989). One mechanism responsible for reciprocal inhibition in antagonistic muscles depends upon the activity of muscle spindle afferents from the agonist muscle, which discharges as the agonist contracts. This agonist muscle spindle discharge activates Ia inhibitory interneurons in the spinal cord, which in turn reduce antagonist anterior horn cell activity. The excitability of these Ia inhibitory interneurons is controlled by supraspinal descending pathways, as is the input in the muscle spindle afferents via presynaptic inhibition (Marsden & Sheehy, 1990). Using the H-reflex technique, reciprocal inhibition can be tested by recording surface EMG responses from relaxed forearm finger flexors elicited by electrically stimulating the median nerve in the cubital fossa and the radial nerve in the spiral groove. They have found that electrical stimulation produced three distinct phases of the reciprocal inhibition of the H-reflex. The timing of the first phase is thought to be Ia disynaptic inhibition of flexor motoneurons (Day *et al.* 1984). It is suggested that the second one reflects presynaptic inhibition of the terminals of flexor Ia afferent fibres (Berardelli *et al.* 1987). The mechanism responsible for the third phase is not fully understood. In comparison with a normal control population, writer's cramp subjects showed the normal reciprocal inhibition in the forearm for the initial phase, but a significant reduction or absence in the second presynaptic phase (Sheehy, Rothwell & Marsden, 1988; Nakashima *et al.* 1989). This observation indicated that there is a defect in presynaptic inhibitory mechanisms in the spinal cord in writer's cramp sufferers.

Stretch reflexes of thumb flexor and triceps in the affected arm have been studied in 16 patients with dystonia and compared with those of a group of age-matched normal subjects during sustained constant contraction (Rothwell *et al.* 1983). Results show that no difference in the size and duration of the long-latency stretch reflex of both

muscles under study was found between subjects with dystonia and neurologically normal individuals.

As indicated in the literature, writer's cramp has been the subject of debate in medical circles for the last century or more (Sheehy & Marsden, 1982). Although various neurophysiological investigations have been undertaken in this area for a large number of years, the underlying physiological mechanisms responsible for abnormality in this condition are poorly understood. One of the main objectives in the present study is to possibly detect some abnormality in the electromyographic patterns of hand muscles in people suffering from writer's cramp, during a series of repetitive finger manipulations akin to handwriting as well as component writing. The dependency of short-latency stretch reflexes on the phase of the movement cycle and the task being performed during various rhythmic movements was examined to test whether there is any defect in peripheral feedback system in subjects with dystonia.

6.2 Results

Results presented in this Chapter are summarised from one of the two writer's cramp subjects, whose case is relatively severe. He participated in all experiments, except Experiment II, since he had difficulty in performing tasks that involved in writing movements which Experiment II mainly consisted of.

EMG activity patterns observed in one writer's cramp subject during simple repetitive finger movement and handwriting

Figure 6.2 shows the raw EMG recordings of muscles FPB and EPB from a normal right-handed subject and a writer's cramp subject during thumb flexion/extension and normal cursive handwriting. Both subjects displayed normal alternating contraction of agonist and antagonist muscles during the simple 'thumb flexion/extension' task (Figure 6.2A and C). During handwriting, the writer's cramp subject resumed the typical co-contraction between thumb flexor and thumb extensor (Figure 6.2D). Alternating contraction of FPB and EPB is clearly observed in the normal healthy subject during handwriting (Figure 6.2B).

Another example is shown in Figure 6.3, illustrating the different movement patterns between a healthy right-handed subject and a writer's cramp subject during 'vertical writing'. EMG phase diagrams of FPB and EPB show remarkably different co-ordination patterns between these two subjects in the execution of the component writing task. The extent of modulation apparently differed between the two subjects. A strong alternation of FPB and EPB activation is observed in the healthy subject. Instead of an alternating activation pattern of agonist and antagonist muscles, the EMG pattern from the writer's cramp subject showed co-activation between FPB and EPB. However, the EMG activity illustrated in Figure 6.2C for the same writer's cramp subject showed the normal alternating EMG activation between agonist and antagonist muscles during 'thumb flexion/extension'. This observation suggests that co-contraction of antagonist muscles does not accompany all voluntary movements. These results agreed that typical

co-contraction with overflow of muscle activity appeared preferentially during more delicate and precision manoeuvres (Rothwell *et al.* 1983). Writer’s cramp is a focal task-specific dystonia.

Stretch reflexes in writer’s cramp

M1 reflex component was strongly elicited in all four muscles: FPB, EPB, FDS and 1DI in the subject with writer’s cramp during constant ‘pen-tip’ task. Figure 6.4 shows that both short- and long-latency reflex responses were evoked in two intrinsic muscles FPB and 1DI, and only the short-latency stretch reflex was elicited in two forearm muscles EPB and FDS for the same subject. However, it is noticeable that the long-latency reflex responses were observed in both antagonist muscles FPB and EPB. The latency of the M2 component, measured as the peak time of the response, appeared to be approximately 75-80 ms in those muscles. In comparison with the normal subjects, the latency in writer’s cramp showed longer than that in normal subjects (Table 5.1). The long-latency responses are more obvious during the rhythmic condition than the constant contraction condition in this subject. Comparable reflex responses elicited in the same group of muscles under dynamic conditions are shown in Figure 6.5. Responses were averaged over all 260 stimuli delivered throughout the recording period, regardless of the phase in which the stimuli occurred.

Table 6.1. Comparison of the size and latency of M1 component in four muscles for 12 normal subjects (mean \pm s.e.m.) and one writer’s cramp subject. The size of the reflex is given as the percentage of the response over the background EMG level during the specified time period.

Muscle	Size (%)		Latency (ms)	
	Normal	Writer Cramp	Normal	Writer Cramp
	n=12	n=1	n=12	n=1
1DI	145.39 \pm 3.98	140.53	30.78 \pm 0.85	30.16
FDS	276.9 \pm 53.18	146.44	20.65 \pm 0.91	24.26
EPB	167.6 \pm 16.37	120.54	22.24 \pm 1.04	24.25
FPB	139.8 \pm 11.46	147.13	30.37 \pm 0.78	36.42

The size and the latency of the M1 component from four muscles for the writer's cramp subject with body height 172 cm are shown in Table 6.1, in comparison with the pooled data from a group of 12 normal subjects with mean height in cm 171.5 ± 7.37 (s.d). Reflex size of FDS and EPB was remarkably reduced in the writer's cramp subject. The size of the responses elicited in two other muscles, FPB and 1DI, appeared to be of similar level between writer's cramp and normal group. The latency of M1 component of all these muscles was increased in the dystonia subject compared to the normal subjects, except the 1DI muscle in which the latency was almost the same between these two.

Phase-dependent modulation of stretch reflex in a dystonia subject

Stretch reflex responses have been shown to be strongly modulated with respect to the phase of the movement cycle in healthy subjects (see Chapter 5). The modulation of reflex responses was investigated in the dystonia subject as well. The responses of 1DI during 'finger abduction/adduction' and FDS during 'pen-tip' are plotted as a function of the cycle phase, illustrated in Figures 6.6 and 6.7 respectively. The reflex response of 1DI muscle during 'finger abduction/adduction' is largely dependent on the phase of the movement. The response within each phase varied approximately in parallel with the background EMG activity in the same phase. Figure 6.7 shows a certain degree of reflex modulation in FDS during the 'pen-tip' task in the dystonia subject, but in a much smaller extent than that in the normal subject (Figure 5.9). There was a weak correlation between the pre-existing muscle activity level and the response elicited within the same phase. In both cases, the averaged background EMG activity reached a peak level preceding the averaged force, due to the muscle contraction.

Task-dependent modulation of reflex response in the same subject

Examples demonstrated in the previous paragraph show the phase-dependent modulation of the reflex responses during rhythmic finger movements. The depth of modulation was largely variable between the two tasks although it may be inappropriate to compare these two situations as different muscles were shown during the two actions.

Here, the reflex modulation and sensitivity are compared between different motor tasks for both FDS and 1DI, respectively. Figure 6.8 illustrates the relationship between the reflex response and the pre-existing muscle activity level of FDS in three tasks and 1DI in two tasks, plotted in X-Y ordinate. The ‘finger press’ task is not shown for 1DI performance due to the absence of a reflex response. For 1DI muscle, the reflex modulation and sensitivity during ‘finger abduction’ are much stronger and higher than during ‘pen-tip’ task. This observation is in correspondence with that obtained in normal subjects. For muscle FDS, the degree of modulation as well as the reflex sensitivity was highest in the ‘finger abduction/adduction’ task, and lowest in the ‘pen-tip’ task,. The reflex patterns for both muscles, therefore, showed certain task-dependency in this subject.

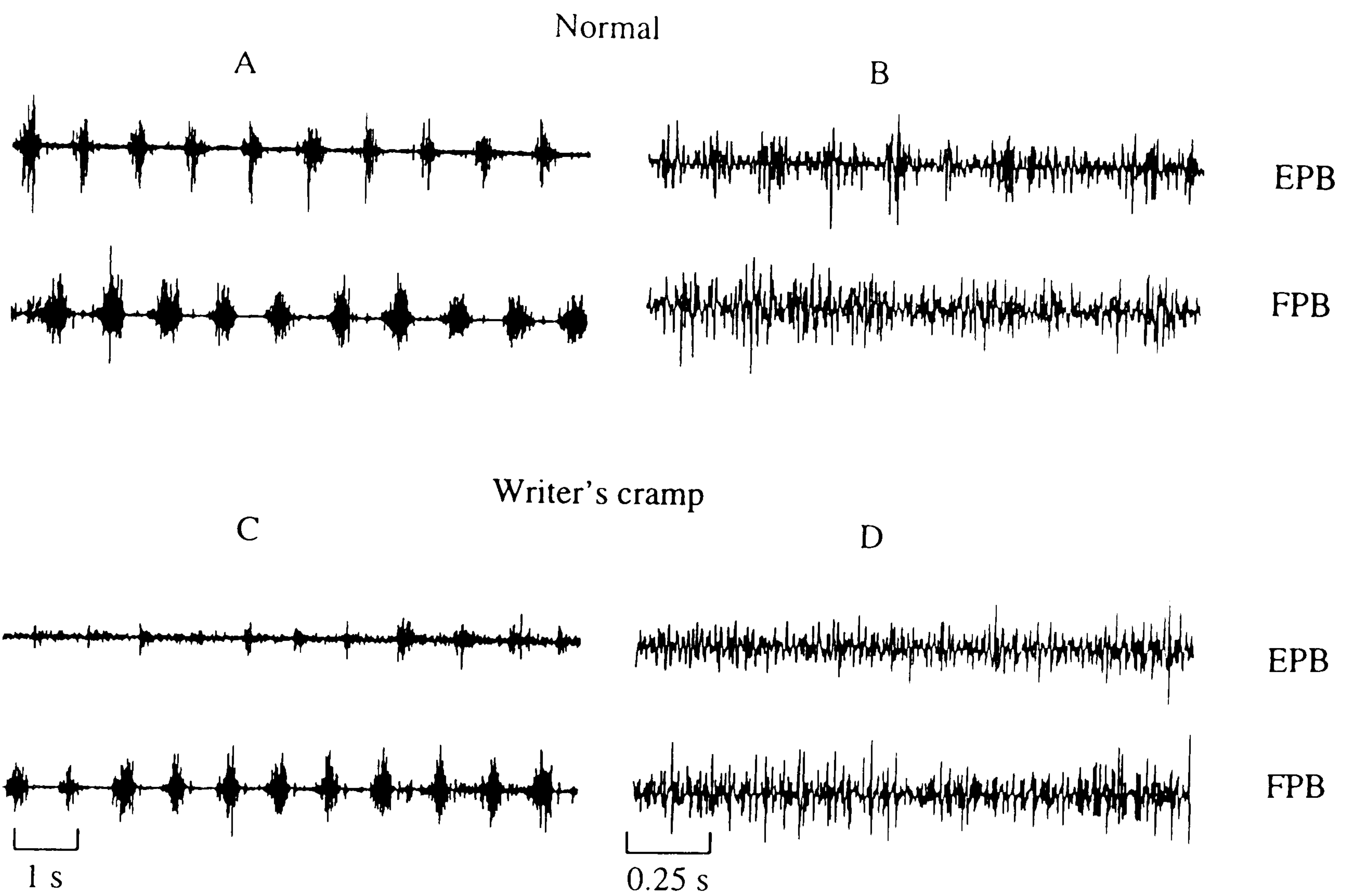


Figure 6.2. Normal reciprocal activation of FPB and EPB for normal right-handed (A) and writer's cramp (C) subjects during thumb flexion and extension. During cursive writing session, typical coactivation between agonist and antagonist muscles is observable in the writer's cramp subject (D).

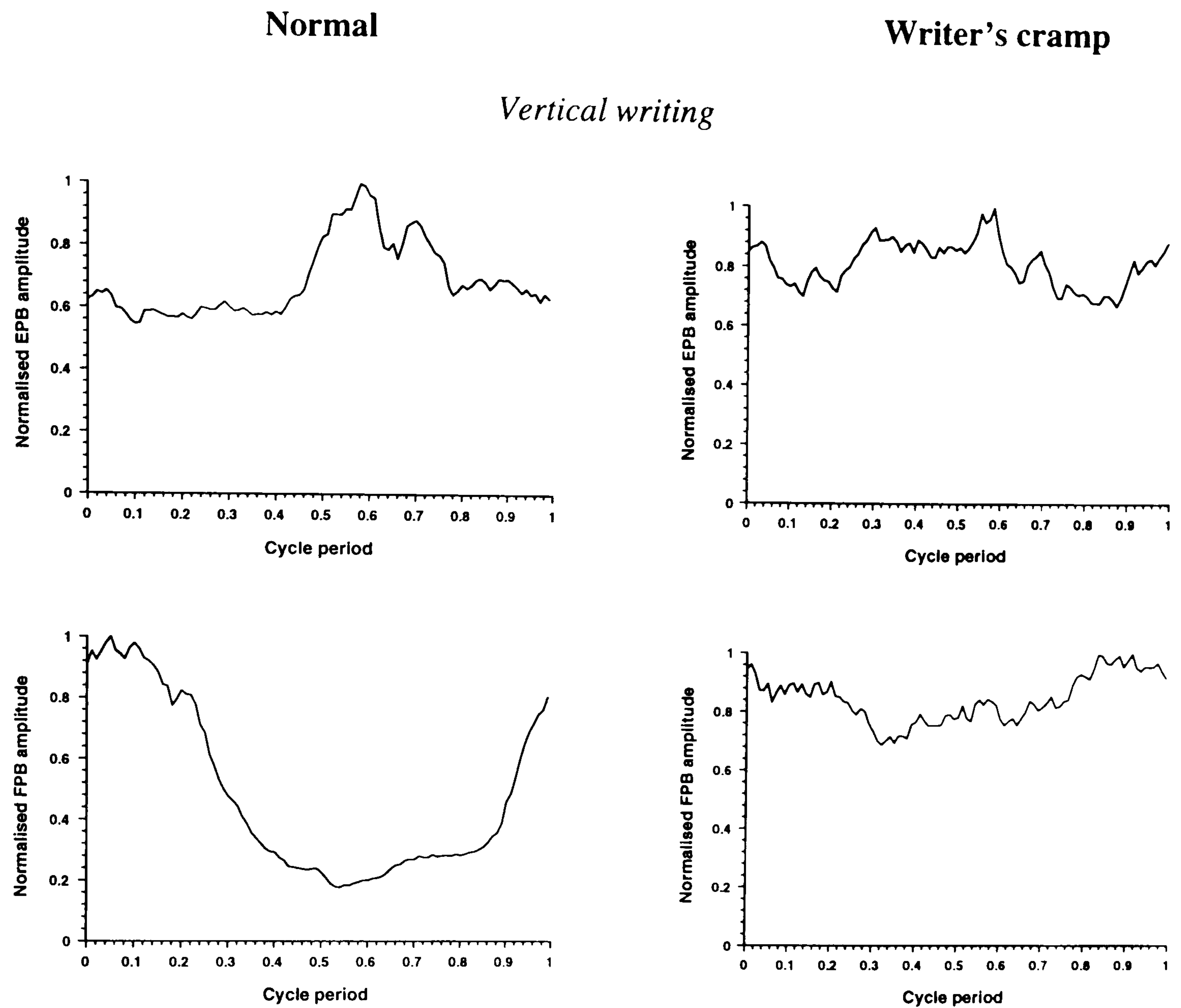


Figure 6.3. EMG phase diagram of FPB (*bottom*) and EPB (*top*) during vertical writing for one healthy subject (left) and one writer's cramp subject (right). Typical normal reciprocal activation between agonist and antagonist was observed in the healthy subject, but not in the writer's cramp subject.

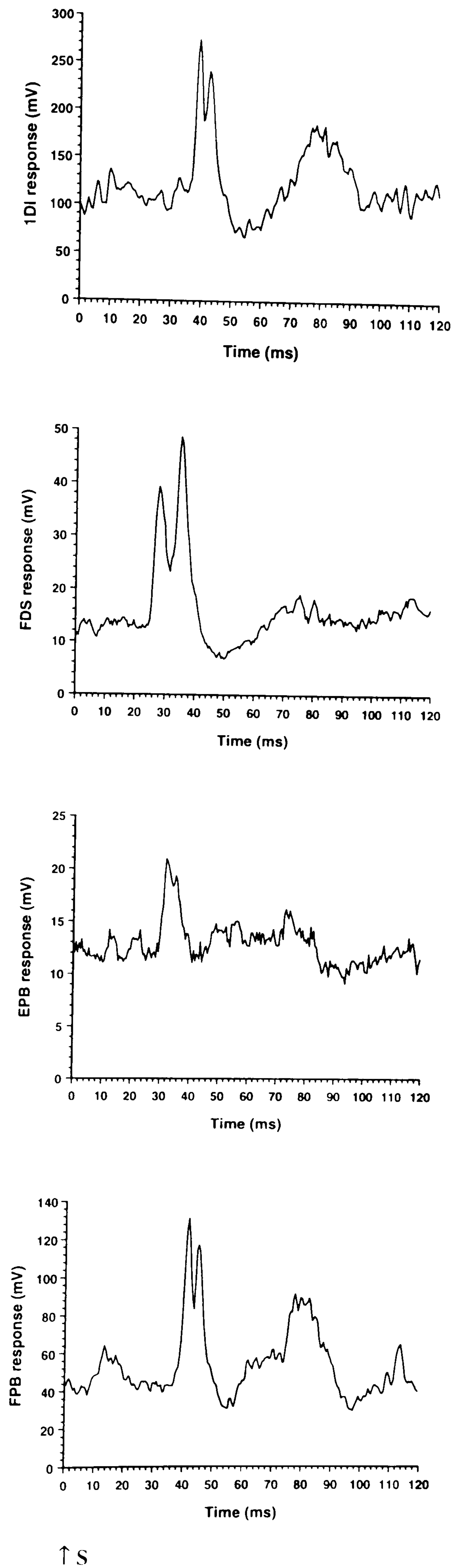


Figure 6.4. Responses evoked in four muscles during constant pen-tip task at 15% MVE for one writer's cramp subject. Stimuli were applied at time zero (*arrow*). Each trace represents an average between 170 sweeps.

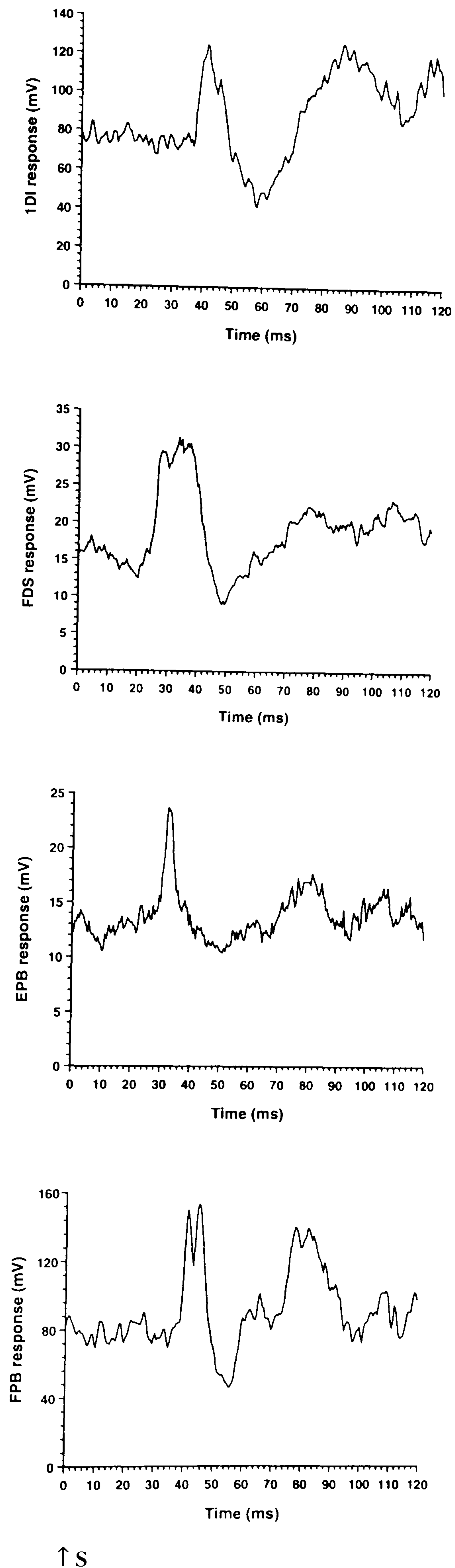
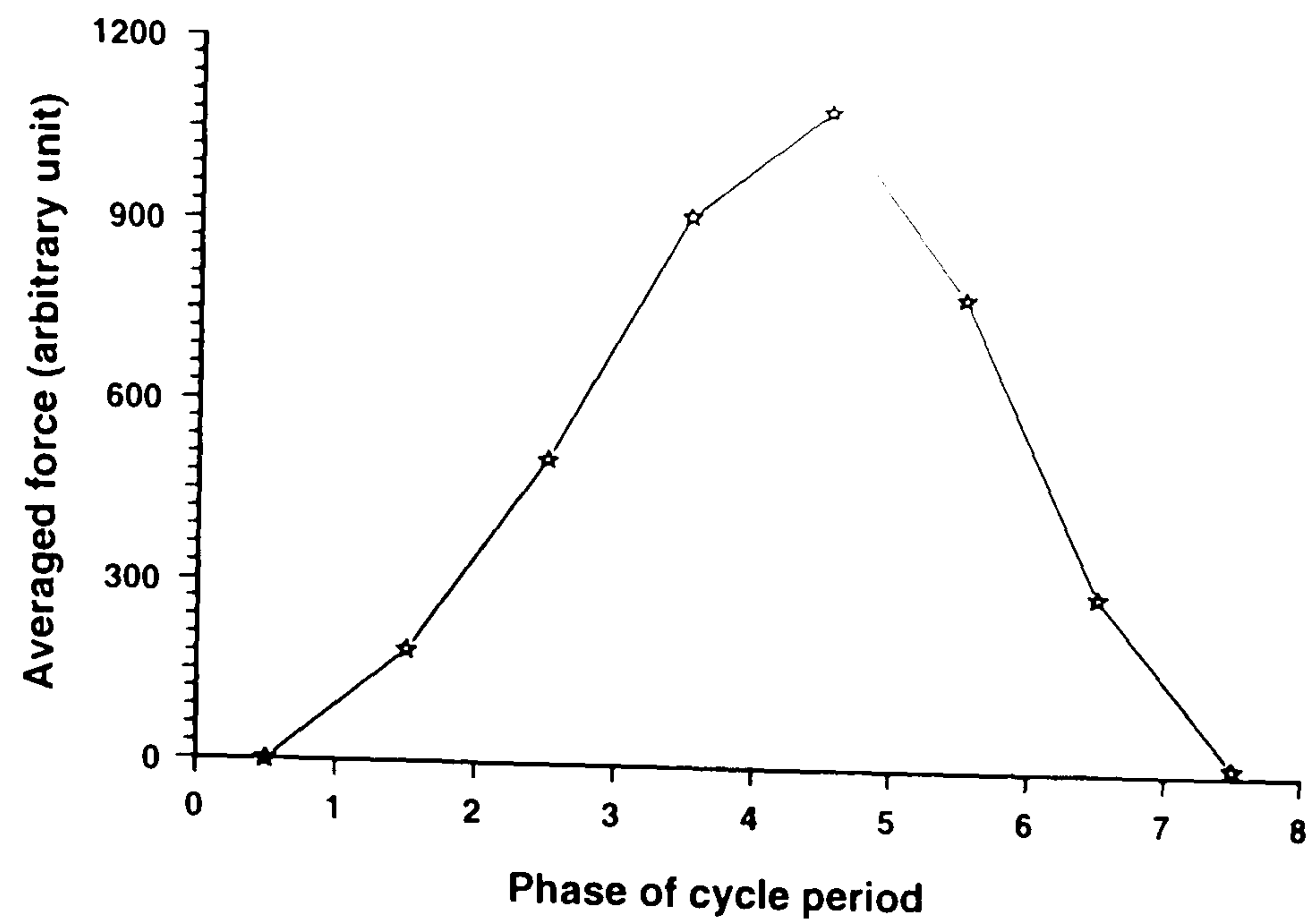
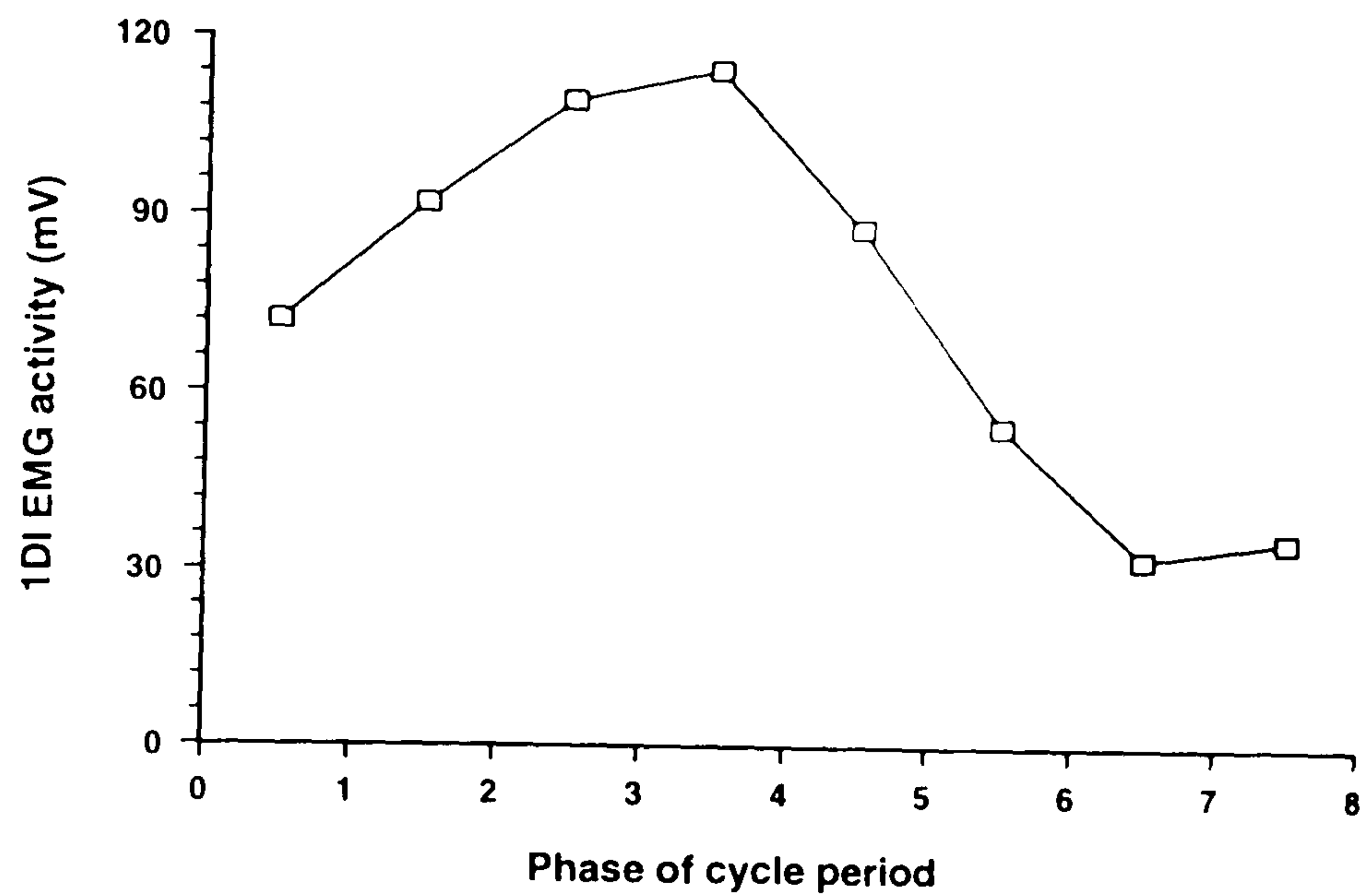


Figure 6.5. Responses elicited in four muscles during dynamic pen-tip task for the same writer's cramp subject. Stimuli were applied at time zero (denoted by *arrow*). Each trace represents an average of all 260 stimuli, irrespective of the phase in which stimuli occurred.

A



B



C

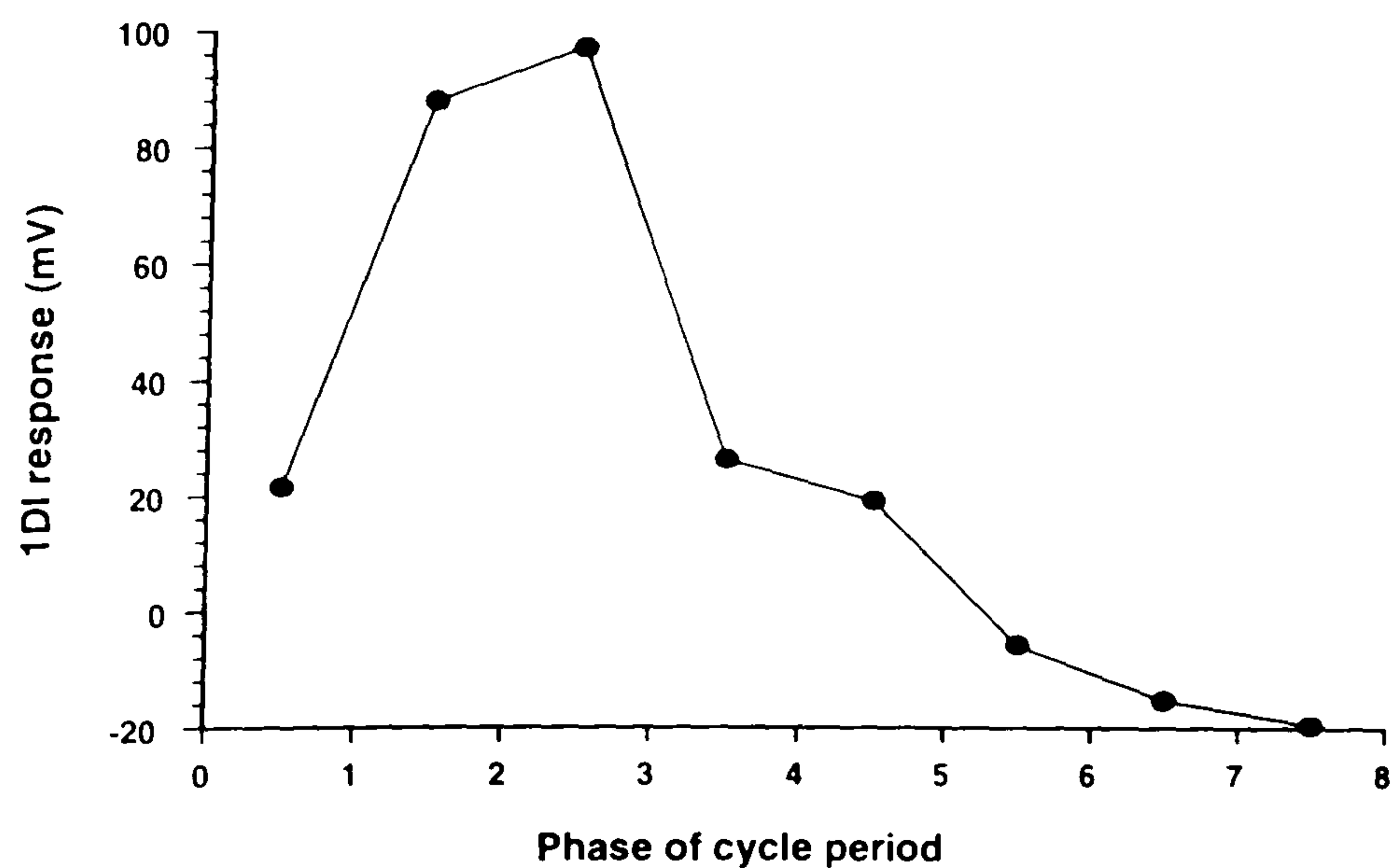
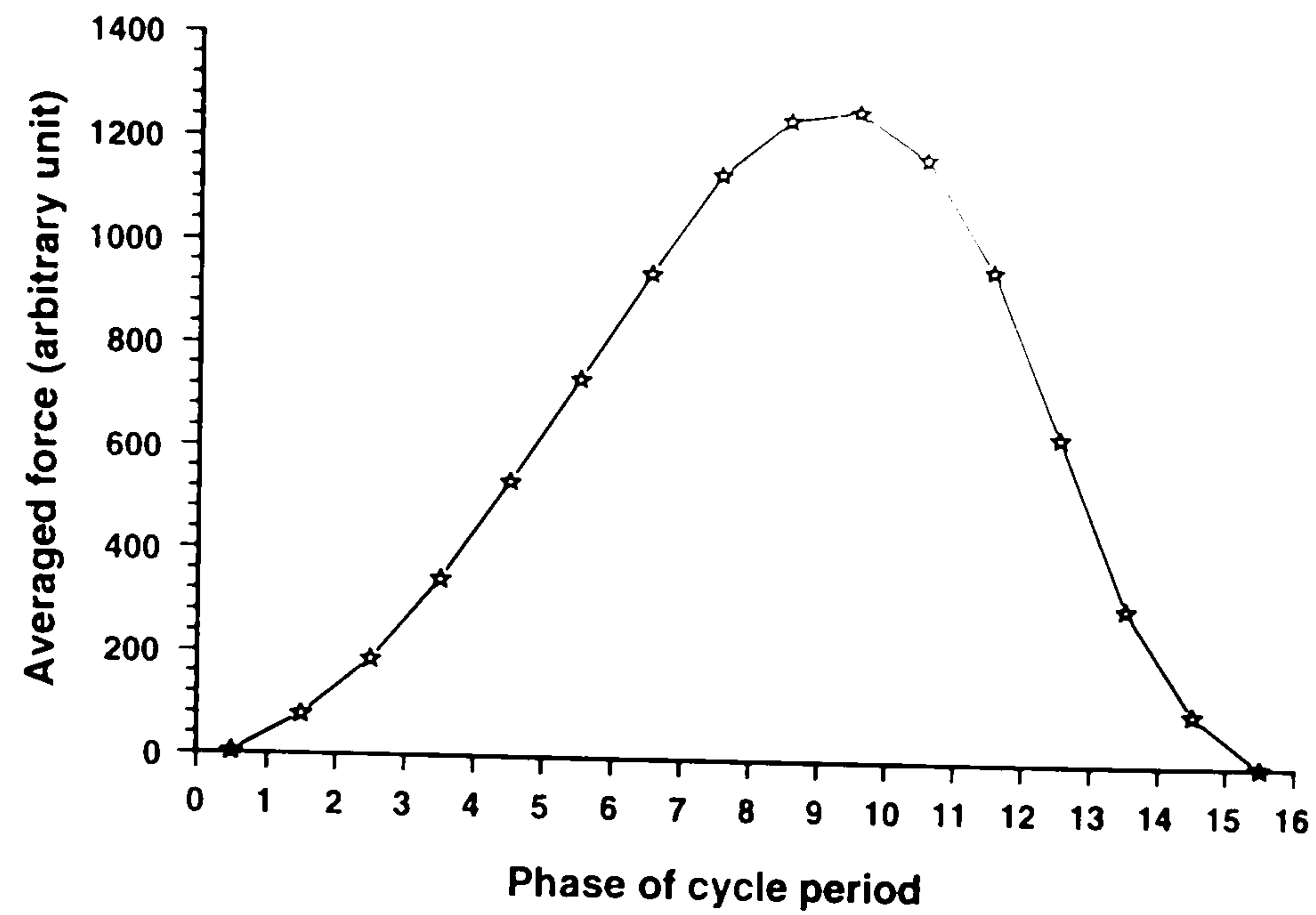
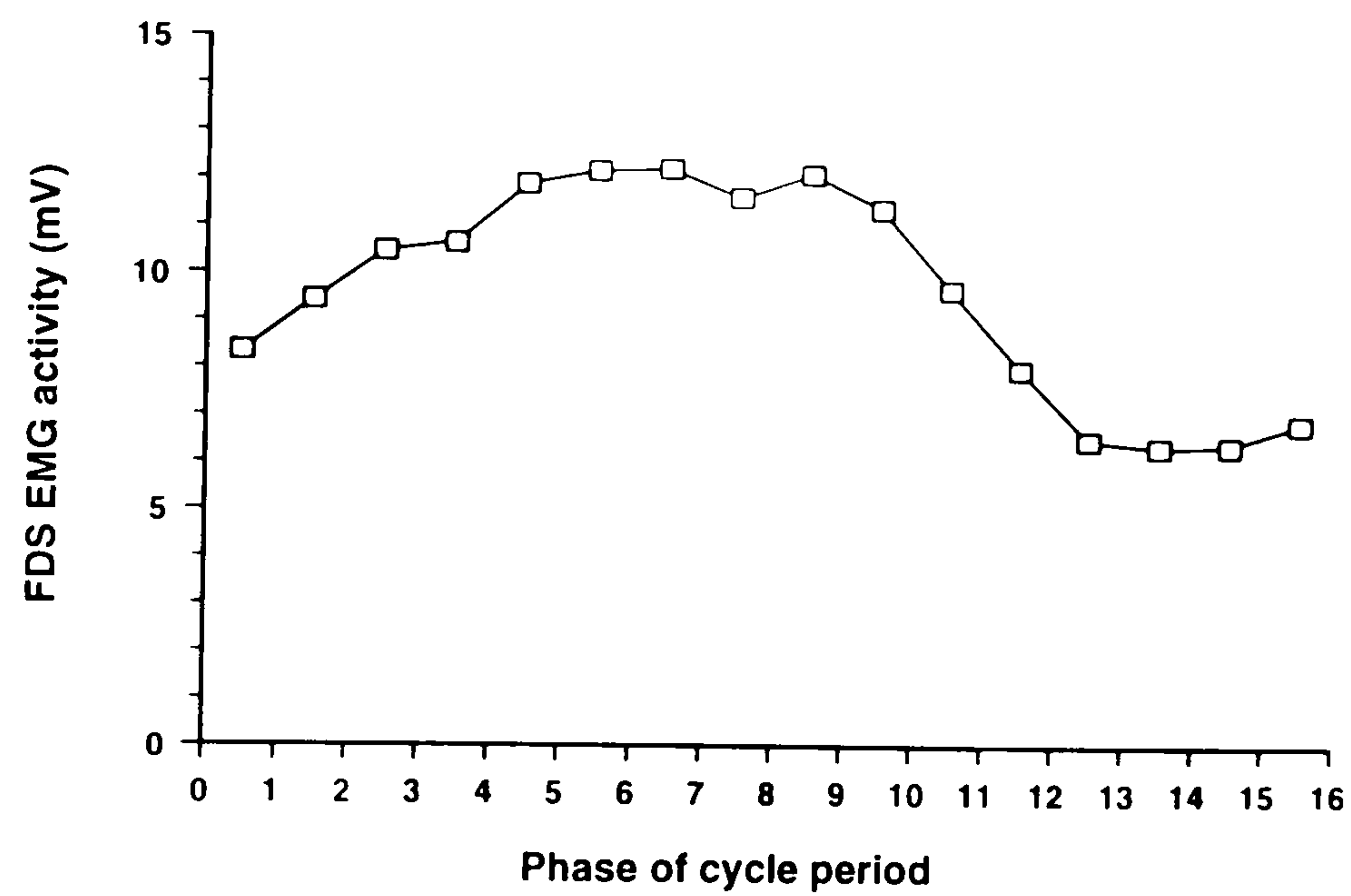


Figure 6.6. Variation of force generated and concomitant EMG activity and reflex responses of 1DI during the finger abduction task for one writer's cramp subject. *A*: Averaged force, and *B*: mean level of EMG activity in 1DI over 30 unperturbed cycles of rhythmic abduction/adduction. *C*: Reflex 1DI responses to all stimuli occurring in each of 8 equal phases.

A



B



C

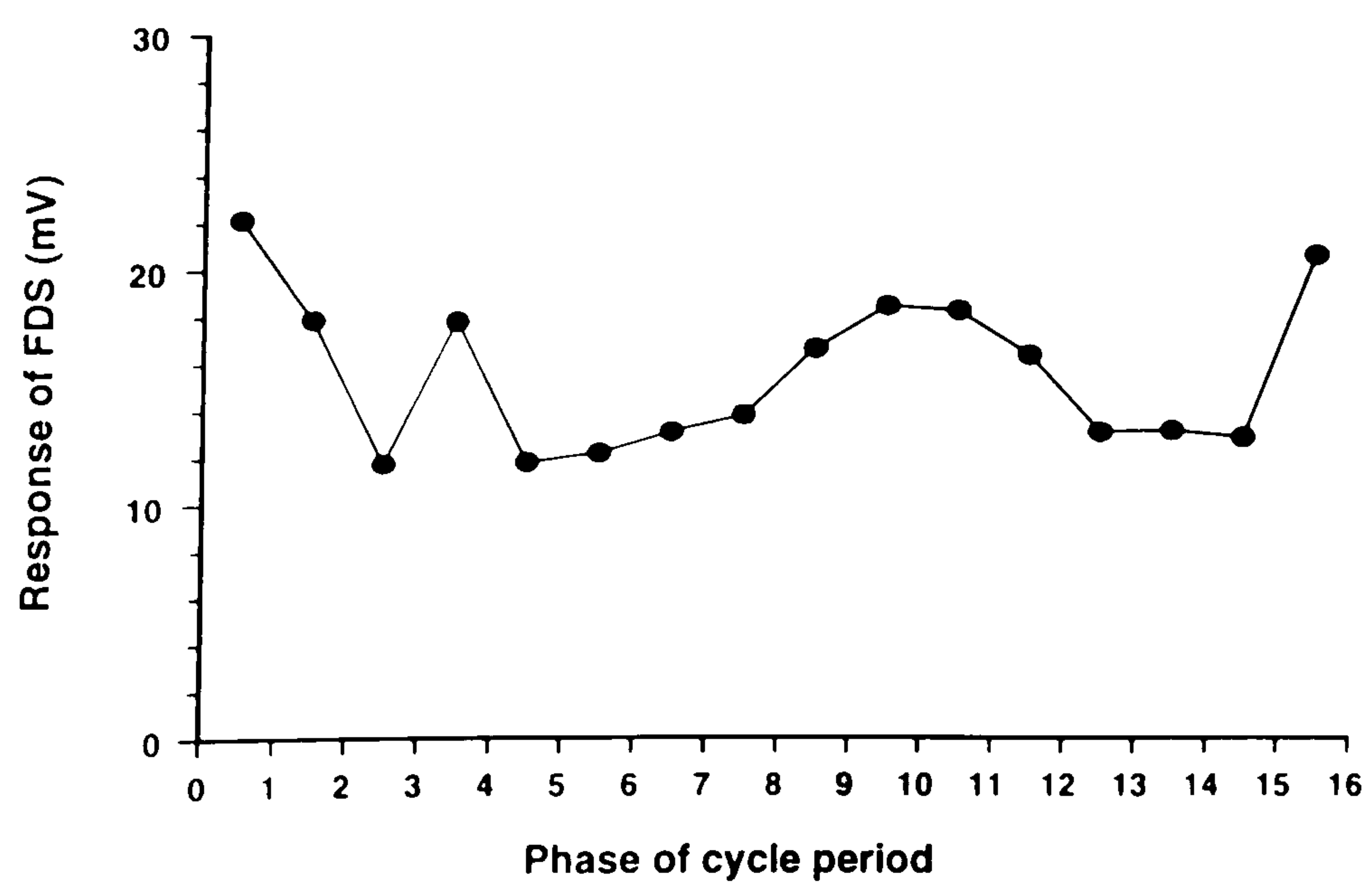


Figure 6.7. Variation of force generated and concomitant EMG activity and reflex responses of 1DI during the pen-tip task for one writer's cramp subject. *A*: Averaged force, and *B*: mean level of EMG activity in FDS over 30 unperturbed movement cycles. *C*: Reflex FDS responses to all stimuli occurring in each of 16 equal phases.

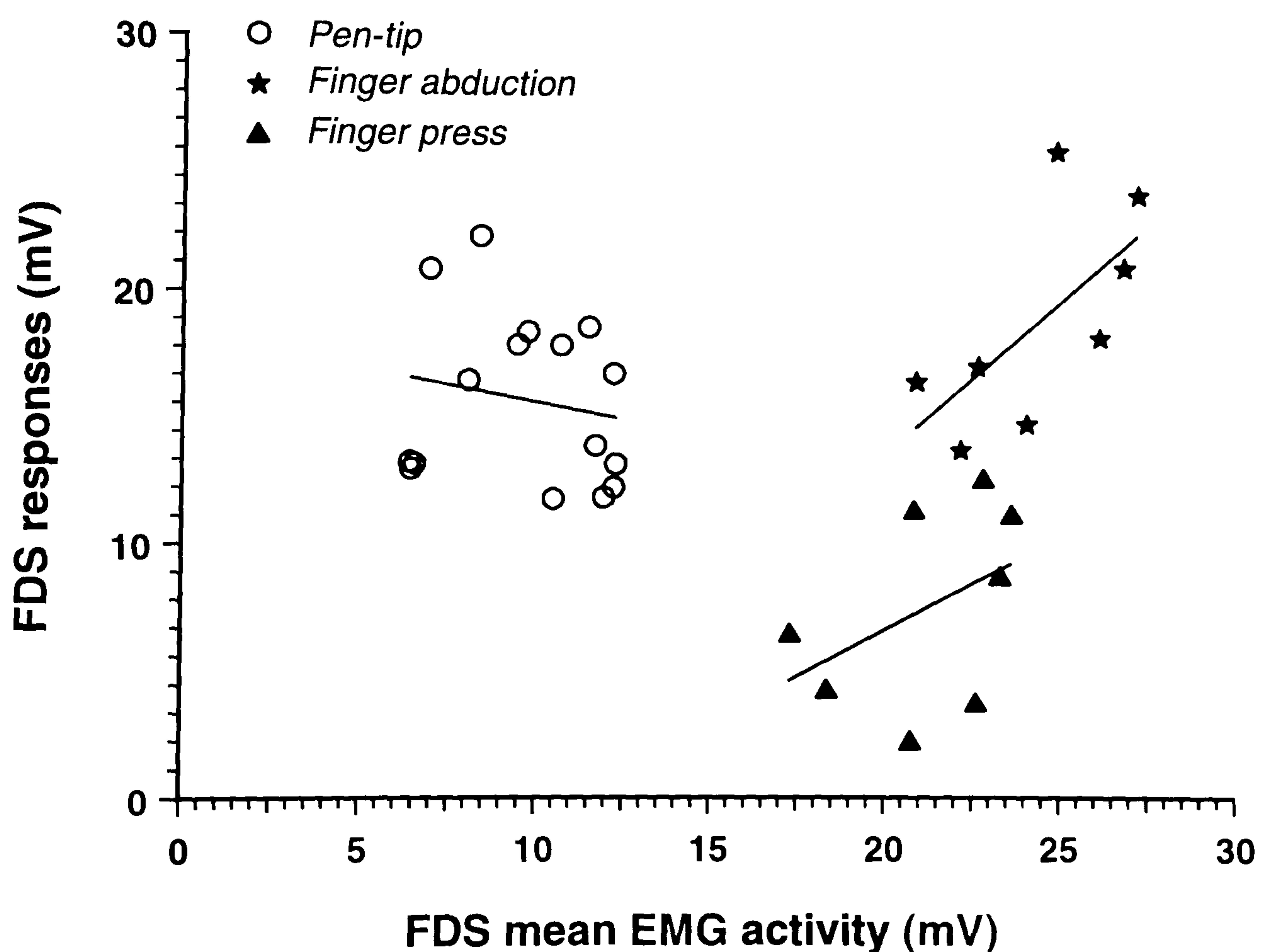
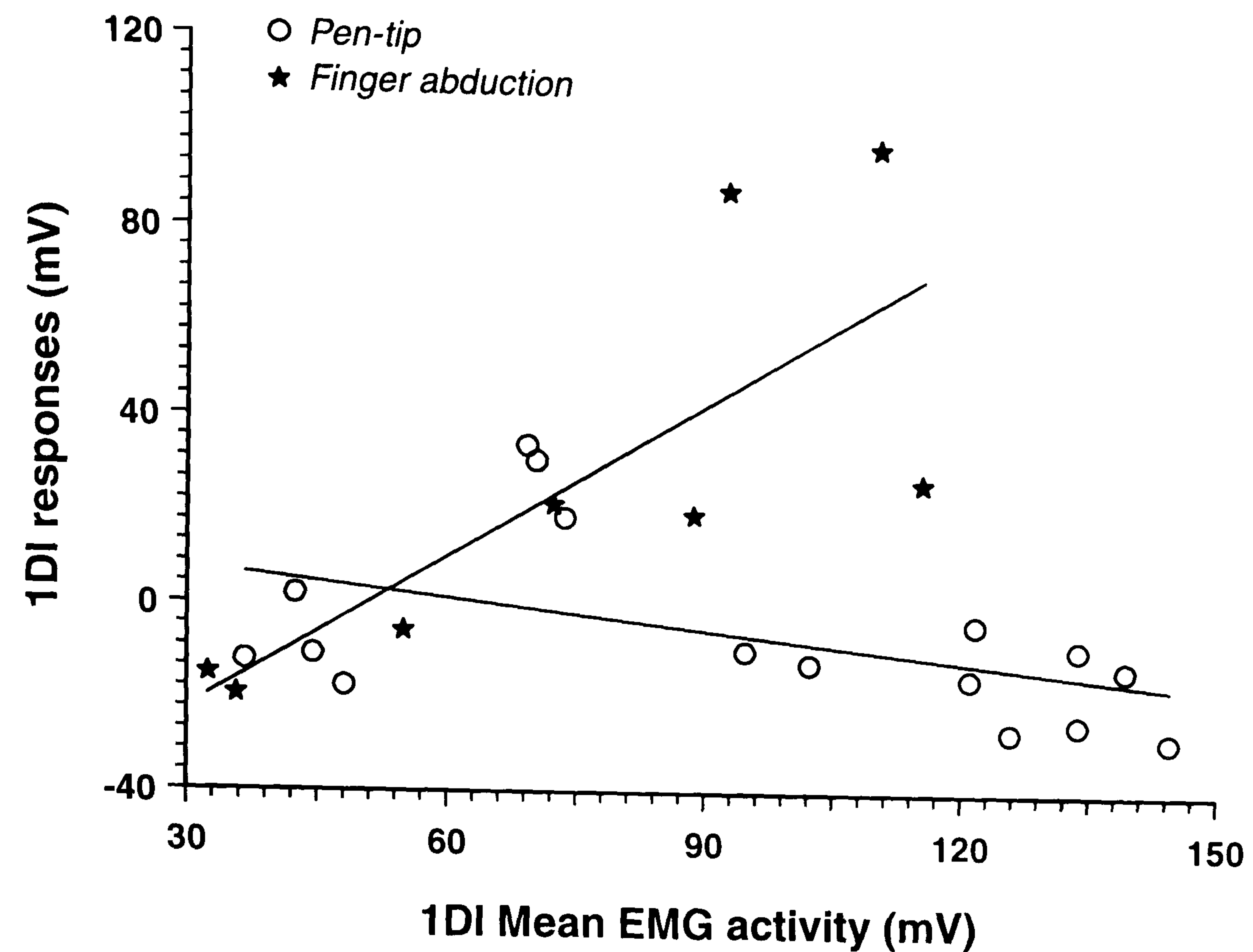


Figure 6.8. Diagrams showing the relationship between the reflex response and the background EMG activity level of 1DI (*Top*) during the two rhythmic tasks, and FDS (*Bottom*) during the three rhythmic tasks in a writer's cramp subject. The slopes for regression lines are -0.216 in 'pen-tip' task (*circle*), 1.088 in 'finger abduction' task (*star*) for 1DI, and -0.267 in 'pen-tip' task (*circle*), 1.227 in 'finger abduction' (*star*), 0.740 in 'finger press' (*triangle*) for FDS, respectively.

6.3 Discussion

It has been noticed for many years that writer's cramp is characterised by co-contraction between antagonistic muscles. This feature was observed in this study as shown in Figure 6.2, illustrating the EMG activities of FPB and EPB during simple 'thumb flexion/extension' and normal handwriting in one writer's cramp subject, in comparison with a normal healthy subject. The co-activation appeared only in writing, not in the other movement, in the writer's cramp subject. As observed during the performance of the tasks, the subject did not show any difficulty in the execution of the 'thumb flexion/extension'. However, he could not maintain writing for even very short periods by his affected hand. He reported the fatigue in his arm after writing a few words. He changed his posture to hold the pen. As described in the Introduction of this chapter, Rothwell *et al.* (1983) have shown that EMG activity of wrist flexors and extensors displayed normal alternating activation during waving, but typical co-contraction during writing in a writer's cramp subject. These electromyographic studies support the view that writer's cramp is a task-specific focal dystonia.

Since writer's cramp was first known more than a century ago, very little attention has been paid to physiological investigations on this condition, especially the reflex behaviour of writer's cramp. In this study, a comparison of the reflex responses was made between writer's cramp and normal subjects under both static and dynamic conditions. During the steady, constant 'pen-tip' task, large similarities were observed in the reflex size and latency between two groups of subjects, reminiscent of the comparison reported by Rothwell *et al.* (1983). They examined the stretch reflex in two upper limb muscles of 16 patients and 11 normal subjects. Compared with normal subjects, there was no change in the size and duration of the long-latency stretch reflex in either of the muscles in patients. In our study, the size and latency of the M1 component were found very close between two groups except the reflex size of FDS and EPB muscles. No statistical comparison could be made due to the single subject included in the writer's cramp group. Responses averaged over all stimuli during the

repetitive 'pen-tip' task also showed a comparable pattern with the reflex responses observed in normal individuals. While the subject performed this task, a three-way force pen was held in his usual pen-grip by his affected hand. He did not report having difficulty in conducting this task. This manual action was not affected by dystonia.

The results shown in the writer's cramp subject indicate that the stretch reflex is, in a certain degree, modulated with respect to both phase and task during repetitive finger motor tasks. In Chapter 5, we have discussed the modulation of the reflex gain during three rhythmic finger manipulations in 12 normal subjects. Previous studies have shown that spinal reflexes are modulated in order to gain the intended movement trajectory during various forms of motor tasks (Belanger & Patla, 1987; Stein & Capaday, 1988). The execution of three learned motor tasks that lasted for 3 minutes was not affected in the subject with writer's cramp. EMG stretch reflexes elicited in the hand muscles to mechanical perturbation show certain degree of modification with respect to both phase and task. It has been accepted that the stereotyped, largely monosynaptic stretch reflex is modified through the action of γ -motoneurons on the receptors, by presynaptic inhibition of the sensory terminals, or by postsynaptic mechanisms acting on the α -motoneurons (Edamura, Yang & Stein, 1991). In a more recent publication, Stein has reviewed human studies on presynaptic inhibition carried out within previous decades (Stein, 1995). It was indicated that presynaptic inhibition plays a role in part of the program for commanding the motor tasks being carried out. The task-dependent modulation is produced by both central pattern generators and sensory feedback that combine to adapt motor patterns under different conditions of voluntary movements by jointly modulating the transmission of information and reflex responses during rhythmic movements. The presynaptic inhibition mechanism was recently investigated between antagonistic muscles of the human forearm in dystonia (Rothwell *et al.* 1983; Sheehy, Rothwell & Marsden, 1988; Nakashima *et al.* 1989). Briefly, the H-reflex of the flexor was tested at different times by stimulating the median nerve at the elbow, before and after a conditioning shock delivered to the extensor's radial nerve. Three distinctive phases of inhibition were observed. Underlying

mechanisms responsible for the initial two phases have been studied (Day *et al.* 1984; Berardelli *et al.* 1987). It was found that in 16 patients with idiopathic writer's cramp or other occupational writer's cramp, the initial disynaptic inhibitory phase was completely normal, whereas the second presynaptic inhibitory phase was significantly reduced in the depth of inhibition. Presynaptic inhibition was also examined in other pathological conditions and found reduced in paraplegics (Calancie *et al.* 1993) and in patients with spastic hemiparesis (Milanov, 1992).

In this study, the modulation pattern of the stretch reflex in a writer's cramp subject did not appear to be obviously different from that observed in normal subjects. Results from the small sample may suggest that the central and peripheral integration regulating and controlling the reflex behaviour during these tasks do not show abnormalities in subjects with this condition. As reported previously, the cause to this condition is dystonia. In order to investigate any likely factors which might contribute to the neurological conditions of writer's cramp, a large population of patients with this condition will be required under the study. The data presented in this chapter gave an indication of the reflex modulation pattern in performing repetitive finger manipulations related to handwriting by one writer's cramp subject, which had not been examined before. One feature which has been noticed is that holding a pen steadily is not affected in writer's cramp whereas writing is affected. This also implies that writer's cramp is a task-specific, movement related disorder.

CHAPTER 7

GENERAL DISCUSSION

Using electrophysiological techniques to record EMG activity, the present study was undertaken to investigate the behaviour of hand muscles during the performance of a variety of rhythmic finger manipulations related to handwriting. Several aspects of muscle activity patterns have been examined, mainly including the motor co-ordination patterns of different hand muscles and the modulation pattern of reflex responses to stimuli while performing voluntary rhythmic finger manipulatory tasks, during repetitive finger manipulations. The importance of the human hand has been emphasised in the beginning of the thesis. However, it is commonly seen in our society that some people suffer from difficulties in using the hand to perform daily tasks, such as writing, typing, and other manipulations. One of these conditions, writer's cramp, has been known for many years, as described in Chapter 6.

To understand the mechanisms underlying the problems with writing or performing other hand manipulations, it is important to establish the muscle activity patterns under normal conditions during the performance of these tasks. On the other hand, very little attention has been paid to investigate how hand muscles work in co-ordination to conduct some rhythmic finger manipulations as well as handwriting. The present study was prompted on the basis of this background. Studies were mostly undertaken on subjects without known neurological diseases. Part of the protocols run in this study were conducted in a few subjects with writer's cramp. Although, due to the shortage of subjects with writer's cramp, it is inappropriate to draw any conclusions about this abnormal condition, this study fills a gap in the area of motor control of the hand in providing some information on rhythmic hand movements and handwriting observed in normal subjects. The main findings obtained in this work include: (1) hand muscles show characteristic co-ordination patterns during the performance of a series of rhythmic manipulatory tasks, and sensory feedback is likely to be intimately involved in the execution of more delicate and skilled movements, e.g. handwriting, in comparison with relatively simple finger movements; (2) reflex responses evoked in hand muscles while performing these rhythmic tasks are highly modulated with respect to both phase of the movement cycle and the nature of the task being carried out.

Co-ordination of hand muscles during voluntary rhythmic movements

Voluntary movement is considered as the most complex kind of motor behaviour, even when it is executed through only a few stages. In contrast to reflex movements, direction and velocity of voluntary movement can be chosen at will and may be changed during the performance of the movement. In the execution of almost all daily activities, such as speaking, chewing, walking and driving, simultaneous movements of different parts of the body are required to co-ordinately work together. Within each individual part of the body, subco-ordination of different muscles that operate the movements of articulation is essentially needed. Successful voluntary movements are based on appropriate co-ordination between different muscles and joints. In the present study, the emphasis has been focused on the motor co-ordination of dominant hand muscles and joints during the performance of discrete and periodic finger actions as well as highly skilled manoeuvres. Co-ordination is largely under voluntary control and is primarily determined by the purpose of voluntary motions. Associated with co-ordination, there exist phenomena of temporal and spatial couplings in muscle groups.

The idea that the cerebellum co-ordinates movement dates back to the last century. Flourens (1824) concluded, following cerebellar ablations in the pigeon, that “the will, the senses, the perception remains, but the co-ordination of movement, the ability for controlled and determined movement, was lost”. This notion was supported by later neurologists (Babinski, 1899, 1906; Holmes, 1939). Many recent studies emphasise primary cerebellar roles in stability control and reflex gain control (MacKay & Murphy, 1979; Thach *et al.* 1986). In the studies by Rispal-Adel *et al.* (1982, 1983), two distinct types of movements, “simple” and “complex” movements, were produced by the electrical stimulation of the baboon’s dentate nucleus. Simple movements usually consist of unidirectional displacement involving a single joint, whereas complex movements are accompanied by the displacement of two or more non-contiguous joints. Both types of movement are considered under the cerebellar control of muscle synergies. Thach, Goodkin & Keating (1992) proposed a model of cerebellar function

on the basis of a review of cerebellar anatomy, neural discharge in relation to behaviour, and focal ablation syndromes. The unique features of this model are the inclusion of new information on (a) the cerebellar output - its replicative representation of body maps in each of the deep nuclei, each coding a different type and context of movement, and each appearing to control movement of multiple body parts more than of single body part; and (b) the newly assessed long length of the parallel fibre, which, by virtue of its connection through Purkinje cells to the deep nuclei, appears optimally designed to combine the actions at several joints and to link the modes of adjacent nuclei into more complex co-ordinated acts. It has been pointed out that many parts of the motor system, including that in the cerebellar cortex, may be involved in different types of motor learning for different purposes. The adaptive role of the cerebellar cortex appears to be specialised for combining simpler elements of movement into more complex synergies, and also in enabling simple, stereotyped reflex systems to respond specifically, appropriately to different task situations (Thach, Goodkin & Keating, 1992).

One of the main findings reported in this study is that muscle activity shows characteristic movement co-ordination patterns between antagonist muscles, and a certain level of co-activation between synergists to maintain the postural balance during the execution of rhythmic voluntary actions, including component writing tasks. Several theoretical models have been proposed to explain the mechanisms of motor co-ordination in relation to the task requirements. One of these models was proposed by Bullock and Grossberg (1988). The basic structure of the model is illustrated in Figure 7.1, which comprises a single channel for an antagonistic pair of muscles. This closed-loop system shows that the difference between the target's position (T) and the current position (P) is first low-pass filtered and then integrated. The GO signal was introduced to multiply the low-pass filtered error, equivalent to a time-dependent gain factor or time constant of the integrator. The output produced by the model is very similar to human targeted movements. This model can be applied to explain the simple repetitive

finger movement investigated in this study, that are primarily under the control of agonist and antagonist muscles.

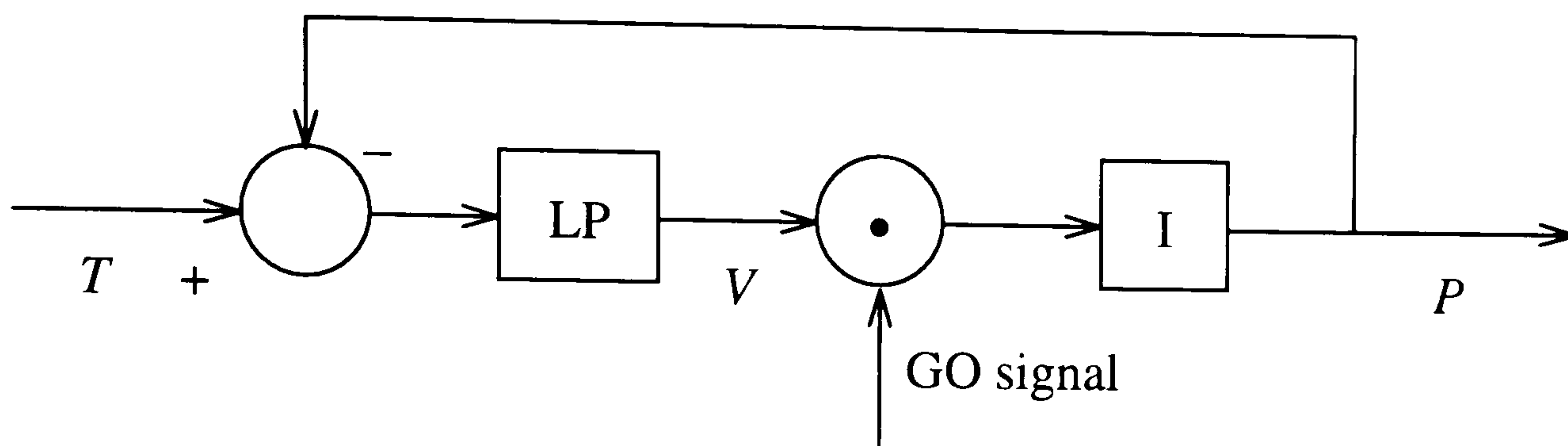


Figure 7.1. Diagram of a channel (lumped channel for an antagonistic pair of muscles) of the model of Bullock & Grossberg (1988). LP: *low pass filter*. I: *integrator*.

To further develop the above model, co-ordination is addressed while the variables T , P and V are considered as vectors rather than scalars. Multiple channels rather than a single channel are considered. The vector components and the channels are associated with various muscles that are involved in the movement. Their start lengths are specified by the current-position vector P at time zero, and their intended final lengths by the target-position T . The difference vector V represents the resultant contribution of each muscle to the targeted movement in terms of both amplitude and direction of the movement. The GO signal is a scalar in principle whereas the variable V is a vector. Otherwise the direction of the movement would be modified by its application. The operation of the GO signal affects that all muscles involved in the movement work in synchrony. The length changes of different muscles are achieved through different velocities. Although synchronous activity of the muscles of a synergy is considered as a fundamental characteristic of motor control, muscle contractions do not always start in strict synchrony. Termination of the activity of the various muscles will be more in synchrony compared with initiation when the components of the target-position vector T change at variable times after the start of the GO signal. The value of the GO signal varies to multiply with the components of the difference vector V for earlier and later-starting muscles. This results from the fact that for later-starting muscles the large initial components of the difference vector V are multiplied with

larger values of the increasing GO signal, thus producing increased initial velocities as compared with an earlier start where the initially large components of V are multiplied by the earlier and smaller values of the GO signal. This model offers a solution for the dynamic aspect of motor equivalence which is contained in the scalar GO signal. The solution can be characterised in a very simple manner in which all muscles are driven by a single signal, the GO signal. The GO signal plays a part in accommodating the velocity between the various muscles by multiplying with different time-dependent factors V (Soechting & Lacquaniti, 1981). Furthermore, physiological studies have found that single-cell activity is related to time-varying movement parameters, including position, velocity and acceleration, and to the direction of the target (Ashe & Georgopoulos, 1994). The activity of the cell is directionally modulated. The activity is the highest for the preferred direction of movement, and decreases gradually when the direction changes to become further away from the preferred one. Cells sharing similar preferred directions tend to have excitatory synaptic interaction whereas cells with opposite preferred directions tend to have inhibitory interactions. It can be reasonably assumed that these effects reflect motor control signals as well as the effects of peripheral inputs. In this study, EMG phase diagrams clearly illustrate the relationship of activation pattern between various muscles. In some tasks, certain muscles appeared to be asynchronous while in others they appeared relatively more synchronous. The pattern observed depends on the function of the muscle in the task in question.

Movement and posture: muscle activity patterns in relation to different postures of pen-holding

As introduced in Chapter 1, the term 'motor control' refers to the study of movements and postures as well as to the function of mind and body that govern movement and posture. Posture, in this context, means the static position of any part of the body. Movement is the transition from one posture to another. Movement and posture are a particular kind of co-ordination in many motor patterns. Movements that serve our particular intentions (e.g. reaching for an object, handwriting, locomotion etc.) frequently change the posture of finger, hand and arm, the angle of the joint, the position

of the centre of mass of the body. Therefore, movements that serve an action's purpose have to be accompanied by adequate postural responses. Experimental work involving single- and multi-joint motions has corroborated the hypothesis that the *CNS* generates movements as a shift of the limb's equilibrium posture. The equilibrium point hypothesis (EP hypothesis) was first proposed by Feldman (1966) who viewed joint posture as an equilibrium resulting from the length-dependent forces generated by agonist-antagonist muscles. A key feature of the EP hypothesis is that muscles have spring-like behaviours.

Motor output patterns in different postures of holding a pen were examined in this study, as described in Chapter 4. During handwriting, a certain posture is used to hold a writing tool. The thumb and fingers made necessary postural reactions to the movement as writing progresses. The results obtained in the study show remarkably similar EMG patterns between DTG and 4FG pen-grips, but different patterns from the 5FG grip. As discussed in Chapter 4, the postures to hold the pen for DTG and 4FG grips appear to be very similar. The posture for these two types of pen grip varied in approximately identical patterns during the performance of the tasks. Another explanation is related to muscle function, which has interpreted the similar modulation patterns of the DTG and opposition. In contrast, 5FG grip presented a remarkably different posture from the DTG and 4FG grips. These results imply the effect of posture on the muscle activity patterns.

Functional implications of reflex behaviour of hand muscles during rhythmic movements

Previous sections have described the reflex behaviour of hand muscles investigated in this study. The main findings include (1) phase-dependent modulation of the reflex response is observed here; (2) the reflex response is modulated depending on the task being carried out; (3) both short-latency (M1) and long-latency (M2) reflex components were elicited in distal hand muscles, and only the short-latency responses were evoked in proximal forearm muscles. The observation of M2 evoked in intrinsic

hand muscles is in line with Phillips' idea that a transcortical reflex loop plays a functional role in distal muscles of the primate (Phillips, 1969). Lemon (1981) and Strick and Preston (1982) have demonstrated that impulses from skin receptors and proprioceptors of the hand are transmitted via oligosynaptic pathways to separate clusters of cells within area 4 of the motor cortex. This fact indicates a distinct functional link between the peripheral input and the cortical output. The combination of spinal stretch reflex and the long-latency stretch reflex is thought to improve the stability in the feedback system. The demand for high stability is particularly great for hand muscles. The implications of multiple reflex pathways for the stability of neuromuscular systems have been discussed previously (Oguztoreli & Stein, 1976).

One of the functional roles of the reflex modulation is to compensate for any changed conditions during the execution of the movement. The evidence in favour of this functional perspective obtained from this study has been presented and discussed in Chapter 5. This effect has been observed in a well-known example of phase-dependent reflex reversal in the spinal walking cat (Forssberg *et al.* 1976). Similar reflex modulation during locomotion in humans has been reported (Belanger & Patla, 1987; Stein & Capaday, 1988). It is summarised that the major functional significance of the reflex is to support voluntary movements, as observed in this study and other previous publications (Stein & Capaday, 1988; Dietz, 1992). The instructions to the voluntary movements are sent out from the brain. To perform precise movements, feedback is normally necessary to fine-tune the central commands. Feedback is more important during manipulation of objects in the environment, when it is impossible to prespecify the exact motor commands before a movement starts. Writing is the movement in which afferent input is essential in order to upgrade motor commands as writing progresses. Thus, muscle activity can be properly scaled to the movement that is required. Deafferented patients have great difficulty to make such movements. They hold the pen very tightly in order to prevent it falling out of their grasp when they write. The fine adjustments of grip which are seen in normal subjects during writing are absent in

deafferented patients (Rothwell, 1994). This is an example typical of the feedback role which is usually assigned to reflexes.

Movement control of handwriting

Handwriting is distinguished from many other motor activities, such as reaching and grasping, maintaining postures, human locomotion, in that it is a learned, highly skilled motor task. Moreover, repetitive movements are employed in handwriting. In recent years, handwriting has gained much attention and several monographs have been contributed to specific areas of handwriting, e.g. biomechanical and computational modelling of trajectory formation (Maarse, 1987; Schmoker, 1991), and educational and developmental aspects (Sassoon, 1988; Meulenbroek, 1989). This study investigated muscle activity patterns during handwriting from the point of view of rhythmic movements as well as motor patterns of hand muscles accompanying different pen grips. Handwriting movement forms a discrete sequence of ballistic movement segments and can be considered as a sequence of discrete actions (Teulings, 1996). Due to this feature and the complexity of cursive script, we exploited some discrete component writing tasks such as repetitive 'vertical writing', 'horizontal writing', 'circle writing' and 'oval writing' to investigate normal handwriting movement, although results obtained from some of the motor tasks are not presented here. EMG patterns of hand muscles were analysed by averaging over the movement cycle. In general, handwriting involves small movement amplitudes and small displacements of the hand. Therefore, the muscle activity patterns appear to be relatively tonic, static and weakly modulated during the performance of movements akin to handwriting.

Right and left-handedness

One of the differences between humans and other members of the animal kingdom is that human kind has a preference for one hand dominated. As is commonly known, most people have the right-hand as the dominant one. A small percentage of the population have dominance of the left-hand. The preference for the right hand in humans is supported by asymmetric structural constraints and accompanied by a higher

degree of skill in nearly all unimanual tasks. In this study, the patterns of muscle activity have been compared between both right and left-handed subjects while conducting rhythmic movements and/or writing by a range of pen-holding styles. Results from this investigation show that muscle activity patterns appear to be comparable between right and left-handed groups. Averaged cyclic EMG activities are highly correlated among those two groups during periodic finger actions and discrete writing. This may suggest that the dominant hand, no matter whether it is the right or left-hand, receives similar motor commands from the central and peripheral nervous system. Therefore, the way in which movements were performed is similar between these two dominances. Another factor is that, to some extent, muscle activity pattern is determined by posture as well. In this study, both right and left-handed subjects employed the same kind of posture to perform tasks. In the writing tasks carried out, no left-handed subject used a hooked writing posture with hyperflexed wrist which is sometimes seen in left-handers.

Handwriting is accompanied by a high level of skill and is performed unimanually. However, it is evident that many simple repetitive finger manipulations are executed by both hands simultaneously. So far, studies have focused only on the dominant hand. Further investigations might be undertaken on the movement co-ordination of both hands in the execution of rhythmic tasks. Although the co-ordination of two hands has been reported previously, these studies mainly centred on the temporal features only, and the muscle activity patterns were neglected. As expected from the notion of hand dominance, performance of the two hands differs in various aspects. Guiard (1987) has provided a detailed analysis of bimanual performance in holding-and-manipulating tasks. Three aspects of functional specialisation were identified. Firstly, the dominant right hand produced movements with higher frequencies and larger amplitudes than the left one. Secondly, in the right-handers, the left hand offers the spatial reference for movements of the right hand. Thirdly, the movements of the two hands are distinguished in both temporal and spatial scales. The left hand should establish the reference before the initialisation of the right hand movements. Guiard (1987), therefore, postulated a left hand precedence in action. In addition, the 'rhythm

dominance' defined by Peters (1981) and Ibbotson and Morton (1981) implies that it is easier to perform simultaneous paced and rapid tapping when the paced tapping is assigned to the left hand and the rapid one to the right than vice versa. These observations appear to be consistent with the hypothesis on the nature of asymmetric structural constraints. It is assumed that some parameters for generalised motor programs, the specific ones, can be set independently for both hands. Figure 7.2 illustrates this hypothesis, which has been supported by experimental results.

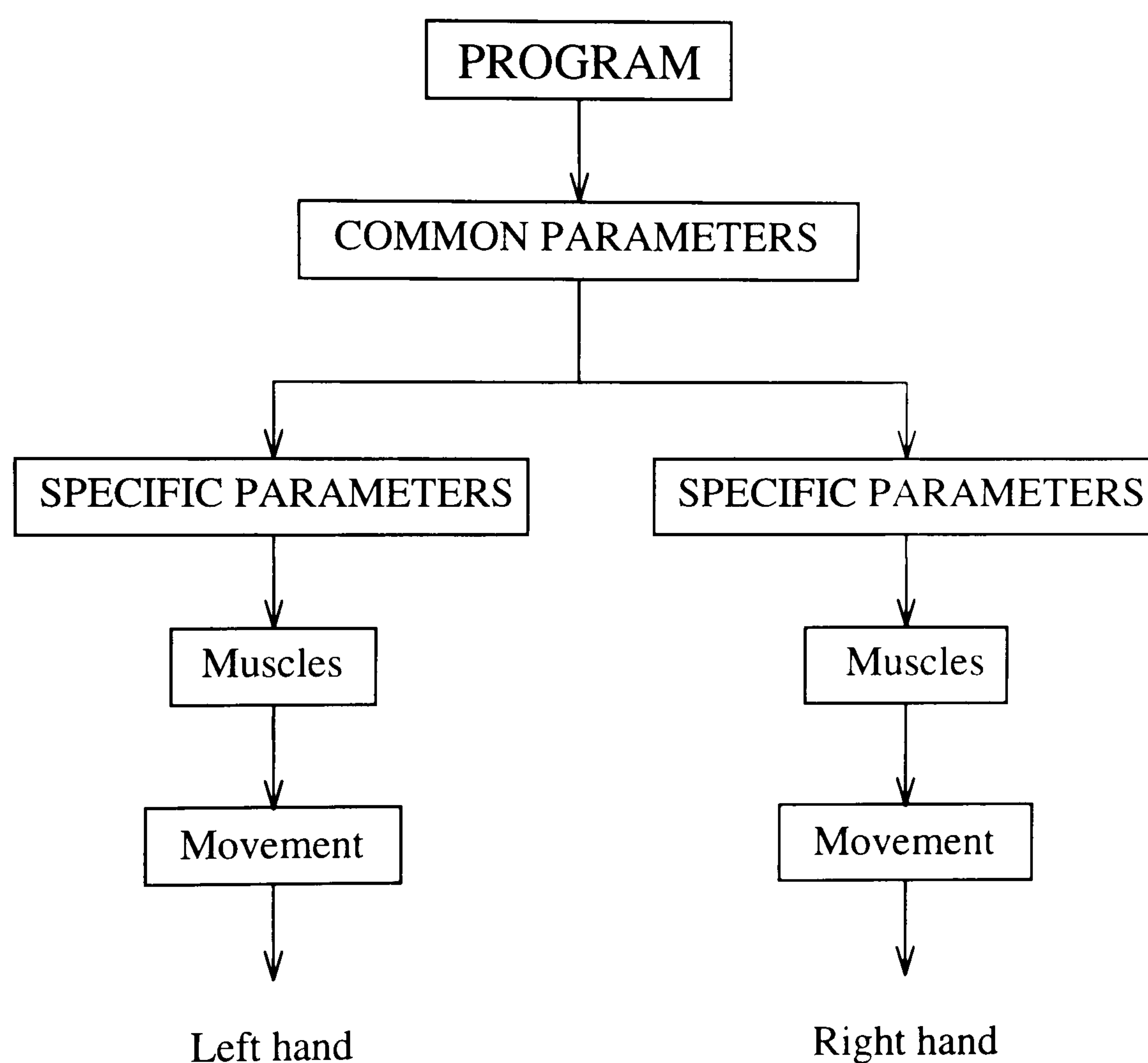


Figure 7.2. The distinction between common and specific parameters of a generalised motor program (Schmidt *et al.* 1979).

Future work to be carried out

Apart from those aspects studied here, further investigations can be proposed to continue this research in several aspects. (1) Six hand/forearm muscles were selected and examined in the present study. In fact, nearly all the hand and forearm muscles are involved in producing precisely controlled movements essential for writing. During the

performance of handwriting, the thumb and fingers require the co-ordination of no less than thirty-six muscles (Williams *et al.* 1989). Therefore, a larger number of muscles, including deep hand and arm muscles, are likely to be of interest as a group for further examination. Regarding the EMG recording, needle electrodes will be employed to record the activity of profundus muscles so that no crosstalk is encountered, especially when small hand muscle activity is recorded. To investigate the co-ordination mechanisms during hand movements, the angular changes representing the various positions of the joint will be monitored by means of electrogoniometers together with the muscle activity. (2) Most work on the reflex behaviour in this study was conducted in association with the stretch reflex. By contrast, H-reflex and cutaneomuscular reflex modulation patterns during a range of finger manipulations have been very little studied. Although some preliminary experimental work on CMR has been done during this study, further research on this topic might be promising to develop in the future. (3) Muscle fatigue has been extensively studied in hand muscles within the previous decades. Studies were generally performed with steady muscle contractions rather than under dynamic conditions. On the other hand, previous physiological studies on writer's cramp have not investigated muscle fatigue, which the writer's cramp subject participating in this study had experienced during the test. Preliminary experiments were performed in some normal subjects in the first year of this study, and a thorough investigation may provide some useful information in the future. (4) As introduced earlier in this thesis, writer's cramp is poorly understood and its mechanism is still under debate. In particular, very little attention has been paid to the physiological study of this condition since it was first recognised over a century ago. A future study, in collaboration with clinical staff in the hospital, can be performed to improve the understanding of the mechanisms responsible for this abnormality. Other focal dystonias, such as typist's cramp, pianist's cramp, and any other movement disorders which are accompanied by hand dysfunction, can be explored in order to develop effective treatment.

Conclusions

Based on the electromyographic techniques, we studied the motor patterns of hand muscles in the execution of rhythmic finger manipulations and handwriting. Several aspects of related features were investigated in this study, performed on subjects without any known neurological disorders, and a small number of writer's cramp subjects. Co-ordination of various hand muscles is characterised by synergistic and antagonistic motor patterns. The reflex response to stimulation is modulated with respect to both phase and task. These features indicate the interactions between central and peripheral nervous systems in the control of rhythmic hand movements. This study provides some information on the physiological aspects of handwriting and relevant rhythmic finger manipulations, to which little attention has been paid previously. With respect to dystonic writer's cramp, future study can be focused on the physiological investigations, given the uncertainty of the pathophysiology and the poor understanding of this condition, to provide valuable information for diagnostic purpose and clinical application.

APPENDIX 1

EMG signal phase average

Each cycle period is divided into an equal number of subdivisions (N). The width of each subdivision depends on the duration of each cycle which may vary during the cyclical movements (Figure 1). The mean EMG amplitude within each subdivision is computed. The same computation was applied to all subdivisions of every cycle. These EMG means for each sequential subdivision over all the successive movement cycles in a task are then averaged to produce the final average phase diagram. Averaged EMG signals are then plotted on a normalised time-base or called phase, with the vertical axes showing either the actual EMG amplitude or normalised to the maximal value for each muscle (Xia & Bush, 1996b).

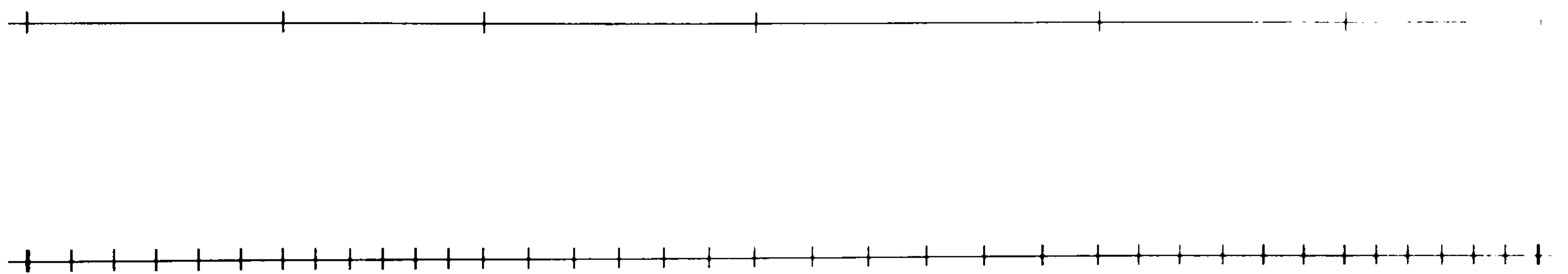


Figure 1. Trigger signal and subdivisions of each cycle. *Top trace:* individual cycles with variable durations, $i = 1, 2, \dots, M$ representing the sequential cycle; *Bottom trace:* subdivisions of each cycle, $j = 1, 2, \dots, N$ representing the subdivisions within each cycle.

The procedure described above is simply expressed using the following matrix and formula:

$$a_{ij} = \begin{matrix} 1,1 & 1,2 & \dots & 1,N \\ 2,1 & 2,2 & \dots & 2,N \\ \dots & \dots & \dots & \dots \\ M,1 & M,2 & \dots & M,N \end{matrix} \quad i = 1, 2, \dots, M; j = 1, 2, \dots, N \quad (1)$$

where a_{ij} is the average EMG amplitude within the j th subdivision of the i th cycle. The averaged EMG amplitude is given as follows:

$$A_j = \sum_{i=1}^M a_{ij} / M \quad j = 1, 2, \dots, N \quad (2)$$

where A_j is the averaged EMG amplitude within the j th subdivision over all cycles

The program used to process EMG phase average was written in CED Spike2 script language. The flowchart of the program operation is illustrated in Figure 2

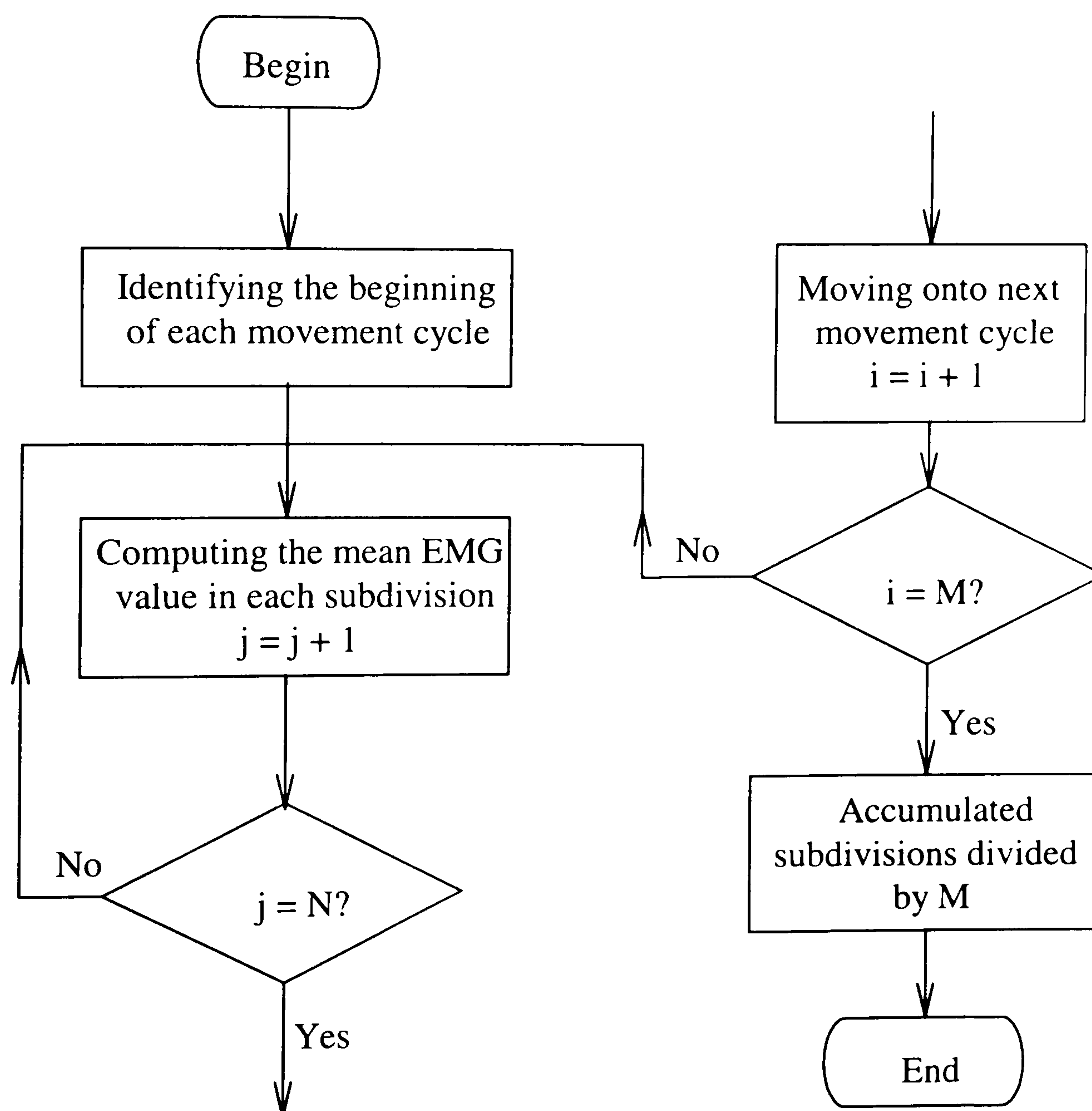


Figure 2. Flowchart of the operation procedure for EMG signal analysis by phase. i represents the movement cycle. j represents the subdivision within each movement cycle. M : total number of movement cycles; N : total number of subdivisions within each cycle (see Figure 1 and Formulas 1, 2).

REFERENCES

Numbers in brackets indicate the chapter(s) in which the referenced work is cited.

- ADAMOVICH, S.V., LEVIN, M.F. & FELDMAN, A.G. (1994). Merging different motor patterns: co-ordination between rhythmical and discrete single-joint movements. *Experimental Brain Research* **99**, 325-337. [1]
- ADRIAN, E.D. & BRONK, D.W. (1929). The discharge of impulses in motor nerve fibres. Part I. Impulses in single fibres of the phrenic nerve. *Journal of Physiology* **66**, 81-101. [1]
- ALSTON, J. & TAYLOR, J. (1987). *Handwriting: Theory, Research and Practice*. Croom Helm Ltd., London. [4]
- AKAZAWA, K., ALDRIDGE, J.W., STEEVES, J.D. & STEIN, R.B. (1982). Modulation of stretch reflexes during locomotion in the mesencephalic cat. *Journal of Physiology* **329**, 553-567. [2, 6]
- ANDERSSON, O., FORSSBERG, H., GRILLNER, S. & WALLEN, P. (1981). Peripheral feedback mechanisms acting on the central pattern generators for locomotion in fish and cat. *Canadian Journal of Physiology and Pharmacology* **59**, 713-726. [3]
- ARMAND, J. (1982). The origin, course and terminations of corticospinal fibres in various mammals. *Progress in Brain Research* **57**, 330-360. [1]
- ASHE, J. & GEORGOPOULOS, A.P. (1994). Movement parameters and neural activity in motor cortex and area 5. *Cerebral Cortex* **6**, 590-600. [7]
- BABINSKI, J. (1899). De l'asynergie cerebelleuse. *Revue Neurologique* **7**, 806-16. [7]
- BABINSKI, J. (1906). Asynergie et inertie cerebelleuses. *Revue Neurologique* **14**, 685-686. [7]
- BASMAJIAN, J.V. & DE LUCA, C.J. (1985). *Muscles Alive: Their Functions Revealed by Electromyography*, 5th edn. Williams & Wilkins, Baltimore. [1]
- BELANGER, M. & PATLA, A.E. (1987). Phase-dependent compensatory responses to perturbation applied during walking in humans. *Journal of Motor Behaviour* **19**, 434-453. [5, 6, 7]
- BERARDELLI, A., DAY, B.L., MARSDEN, C.D. & ROTHWELL, J.C. (1987). Evidence favouring presynaptic inhibition between antagonist muscles afferents in the human forearm. *Journal of Physiology* **391**, 71-83. [6]
- BERGMANN, K.P. (1990). Incidence of atypical pencil grasps among non-dysfunctional adults. *The American Journal of Occupational Therapy* **44**, 736-740. [4]
- BERNE, R.M. & LEVY, M.N. (1993). *Physiology*, 3rd edn. Mosby, St Louis. [3]
- BERNSTEIN, N.A. (1936). Die Kymozyclographische Methode der Bewegungsuntersuchung. In *Handbuch der Biologischen Arbeitsmethoden*, ed. ABDERHALDEN, E., pp. 629-680. Urban & Schwarzenberg, Wien. [1]
- BIGLAND-RITCHIE, B., JOHANSSON, R., LIPPOLD, O.C.J. & WOODS, J.J. (1983). Contractile speed and EMG changes during fatigue of sustained maximal voluntary contraction. *Journal of Neurophysiology* **50**, 313-325. [3]

- BIGLAND-RITCHIE, B. & LIPPOLD, O.C.J. (1954). The relation between force, velocity, and integrated electrical activity in human muscles. *Journal of Physiology* **123**, 214-224. [2]
- BOEHME, R. (1988). *Improving upper body control*. Therapy Skill Builders, Tucson. [4]
- BRAUN (1897). *Annals of Physical Chemistry* **60**, 552. [1]
- BREMNER, F.D., BAKER, J.R. & STEPHENS, J.A. (1991). Effect of task on the degree of synchronisation of intrinsic hand muscle motor units in man. *Journal of Neurophysiology* **66**, 2072-2083. [1, 3]
- BROOKE, J.D., CHENG, J., MISIASZEK, J.E. & LAFFERTY, K. (1995). Amplitude modulation of the soleus H reflex in the human during active and passive stepping movements. *Journal of Neurophysiology* **73**, 102-111. [1, 5]
- BROOKS, V.B. (1986). Motor control. In *The Neural Basis of Motor Control*, ed. BROOKS, V.B., pp. 5-17. Oxford University Press, Oxford. [1]
- BROWN, T.G. (1911). The intrinsic factors in the act of progression in the mammal. *Proceedings of the Royal Society* **B84**, 308-319. [1]
- BROWN, T.G. (1914). On the nature of the fundamental activity of the nervous centres: together with an analysis of the conditioning of rhythmic activity in progression, and a theory of the evolution of function in the nervous system. *Journal of Physiology* **48**, 18-46. [1, 3]
- BUCHHOLZ, B. & ARMSTRONG, T.J. (1992). A kinematic model of the human hand to evaluate its prehensile capabilities. *Journal of Biomechanics* **25**, 149-162. [3]
- BULLOCK, D. & GROSSBERG, S. (1988). Neural dynamics of planned arm movements: Emergent invariants and speed-accuracy properties during trajectory formation. *Psychological Review* **95**, 49-90. [7]
- BUNNELL, S. (1948). *Surgery of the Hand*, 2nd edn. J.B. Lippincott Company, Philadelphia. [1]
- BURKE, D., GRACIES, J.M., MAZEVET, D., MEUNIER, S. & PIERROT-DESEILLIGNY, E. (1992a). Convergence of descending and various peripheral inputs onto common propriospinal-like neurones in man. *Journal of Physiology* **449**, 655-671. [1]
- BURKE, D., GRACIES, J.M., MEUNIER, S., PIERROT-DESEILLIGNY, E. (1992b). Changes in presynaptic inhibition of afferents to propriospinal-like neurones in man during voluntary contractions. *Journal of Physiology* **449**, 673-687. [1]
- CACCIA, M.R., MCCOMAS, A.J., UPTON, A.R.M. & BLOGG, T. (1973). Cutaneous reflexes in small muscles of the hand. *Journal of Neurology, Neurosurgery and Psychiatry* **36**, 960-977. [1, 5]
- CALANCIE, B., BROTON, J.G., KLOSE, K.J., TRAAD, M., DIFINI, J. & AYYAR, D.R. (1993). Evidence that alterations in presynaptic inhibition contribute to segmental hypo- and hyperexcitability after spinal cord injury in man. *Electroencephalography and Clinical Neurophysiology* **89**, 177-186. [6]
- CAPADAY, C. & STEIN, R.B. (1986). Amplitude modulation of the soleus H reflex in the human during walking and standing. *Journal of Neuroscience* **6**, 1308-1313. [1, 5]
- CAPADAY, C. & STEIN, R.B. (1987). Difference in the amplitude of the human soleus H reflex during walking and running. *Journal of Physiology* **392**, 513-522. [1, 5]

- CHAMBERS, W.W. & SPRAGUE, J.M. (1951). Differential effects of cerebellar anterior lobe cortex and fastigial nuclei on postural tones in the cat. *Science* **114**, 324-25. [3]
- CLOSE, J.R. & KIDD, C.C. (1969). The functions of the muscles of the thumb, the index and the long fingers. *Journal of Bone and Joint Surgery* **51**, 1601-1620. [1]
- CODY, F.W.J., LÖVGREEN, B. & SCHADY, W. (1993). Increased dependence upon visual information of movement performance during visuo-motor tracking in cerebellar disorders. *Electroencephalography and Clinical Neurophysiology* **89**, 261-268. [3]
- COLE, K.J. & ABBS, J.H. (1986). Co-ordination of three-joints digit movements for rapid finger-thumb grasp. *Journal of Neurophysiology* **55**, 1407-1423. [3]
- CRISP, A.H. & MOLDOFSKY, H. (1965). A psychosomatic study of writer's cramp. *British Journal of Psychiatry* **111**, 841-858. [6]
- DARLING, W.G. & COLE, K.J. (1990). Muscle activation patterns and kinetics of human index finger movements. *Journal of Neurophysiology* **63**, 1098-1108. [1, 3]
- DARLING, W.G., COLE, K.J. & MILLER, G.F. (1994). Co-ordination of index finger movements. *Journal of Biomechanics* **27**, 479-491. [3]
- DARTON, K., LIPPOLD, O.C.J., SHAHANI, M. & SHAHANI, U. (1985). Long-latency spinal reflexes in humans. *Journal of Neurophysiology* **53**, 1604-1618. [1, 5]
- DAY, B.L., MARSDEN, C.D., OBESO, J.A. & ROTHWELL, J.C. (1984). Reciprocal inhibition between the muscles of the human forearm. *Journal of Physiology* **349**, 519-534. [6]
- DE LUCA, C.J. & MAMBRITO, B. (1987). Voluntary control of motor units in human antagonist muscles: Co-activation and reciprocal activation. *Journal of Neurophysiology* **58**, 525-542. [3]
- DIETZ, V. (1992). Human neuronal control of automatic functional movements: Interaction between central programs and afferent input. *Physiological Reviews* **72**, 33-69. [1, 5]
- DIETZ, V., DISCHER, M. & TRIPPEL, M. (1994). Task-dependent modulation of short- and long-latency electromyographic responses in upper limb muscles. *Electroencephalography and Clinical Neurophysiology* **93**, 49-56. [5]
- DIETZ, V., FAIST, M. & PIERROT-DESEILLIGNY, E. (1990). Amplitude modulation of the quadriceps H-reflex in the human during the early stance phase of gait. *Experimental Brain Research* **79**, 221-224. [1, 5]
- DIETZ, V. & NOTH, J. (1983). Significance of spinal stretch reflexes in human locomotion. In *Regulatory functions of the CNS: Motion and Organisation Principles*, ed. SZENTAGOTHAÏ, J., PALKOWITS, J. & HAMORI, J., pp. 169-177. Pergamon Press, Oxford. [1]
- DIETZ, V., SCHMIDTBLEICHER, D. & NOTH, J. (1979). Neuronal mechanisms of human locomotion. *Journal of Neurophysiology* **42**(5), 1212-1222. [1]
- DOEMGES, F. & RACK, P.M.H. (1992a). Changes in the stretch reflex of the human first dorsal interosseous muscle during different tasks. *Journal of Physiology* **447**, 563-573. [1, 5]
- DOEMGES, F. & RACK, P.M.H. (1992b). Task-dependent changes in the response of human wrist joints to mechanical disturbance. *Journal of Physiology* **447**, 575-585. [1, 5]

- DUBOIS-REYMOND, E. (1849). Untersuchungen über Thierische Elektrizität, Vol. II. second part. Verlag von G. Reimer, Berlin. [1]
- DUCHENNE, G.B.A. (1867). *Physiologie des Mouvements*. English edition translated by KAPLAN, EB (1956) *Physiology of Movements*. W.B. Saunders Company. Philadelphia. [1]
- DUFRESNE, J.R., SOECHTING, J.F. & TERZUOLO, C.A. (1980). Modulation of the myotatic reflex gain in man during intentional movements. *Brain Research* **24**, 245-255. [5]
- DUYSENS, J. & STEIN, R.B. (1978). Reflexes induced by nerve stimulation in walking cats with implanted cuff electrodes. *Experimental Brain Research* **197**, 538-542. [1]
- EDAMURA, M., YANG, J.F. & STEIN, R.B. (1991). Factors that determine the magnitude and time course of human H-reflexes in locomotion. *Journal of Neuroscience* **11**, 420-427. [1, 5, 6]
- EDIN, B.B., WESTLING, G. & JOHANSSON, R.S. (1992). Independent control of human finger-tip forces at individual digits during precision lifting. *Journal of Physiology* **450**, 547-564. [3]
- ENGBERG, I. & LUNDBERG, A. (1969). An electromyographic analysis of muscle activity in the hindlimb of the cat during unrestrained locomotion. *Acta Physiologica Scandinavica* **75**, 614-630. [1]
- ENOKA, R.M., ROBINSON, G.A. & KOSSEV, A.R. (1989). Task and fatigue effects on low-threshold motor units in human hand muscle. *Journal of Neurophysiology* **62**, 1344-1359. [3]
- ERB, W. (1875). Über Sehnenreflexe bei Gesunden und bei Rückenmarkskranken. *Archiv für Psychiatrie* **5**, 792-802. [1]
- ERHARDT, R.P. (1982). Developmental prehension assessment. RAMSCO, Laurel, MD. [4]
- EVANS, A.L., HARRISON, L.M. & STEPHENS, J.A. (1989). Task-dependent changes in cutaneous reflexes recorded from various muscles controlling finger movement in man. *Journal of Physiology* **418**, 1-12. [1, 5]
- EVANS, A.L., HARRISON, L.M. & STEPHENS, J.A. (1990). Maturation of the cutaneomuscular reflex recorded from the first dorsal interosseous muscle in man. *Journal of Physiology* **428**, 425-440. [5]
- FAIRBANK, A. (1970). *The Story of Handwriting: Origins and Development*. Faber, London. [1]
- FELDMAN, A.G. (1966). Functional tuning of the nervous system during control of movement or maintenance of a steady posture. III Mechanographic analysis of the execution by man of the simplest motor task. *Biophysics* **11**, 766-775. [7]
- FLOURENS, P. (1824). *Recherches experimentales sur les propriétés et les fonctions du système nerveux, dans les animaux vertébrés*. Crevot, Paris. [3, 7]
- FOERSTER, O. (1921). *Zeitschrift für die gesamte Neurologie und Psychiatrie*. **73**, 1-169. [1, 6]
- FORBES, A. & THACHER, C. (1920). *American Journal of Physiology* **52**, 409. [1]

- FORSSBERG, H. (1979). Stumbling corrective reaction: A phase-dependent compensatory reaction during locomotion. *Journal of Neurophysiology* **42**, 936-953. [5]
- FORSSBERG, H., GRILLNER, S. & ROSSIGNOL, S. (1975). Phase dependent reflex reversal during walking in chronic spinal cats. *Brain Research* **85**, 103-107. [1, 5]
- FORSSBERG, H., GRILLNER, S. & ROSSIGNOL, S. (1977). Phasic gain control of reflexes from the dorsum of the paw during spinal locomotion. *Brain Research* **132**, 121-139. [1, 5]
- FORSSBERG, H., GRILLNER, S. & ROSSIGNOL, S. & WALLEN, P. (1976). Phasic control of reflexes during locomotion in vertebrates. In *Neural Control of Locomotion*, ed. HERMAN, R.M., GRILLNER, S., STEIN, P.S.G. & STUART, D.G., pp. 647-674. Plenum Press, New York. [7]
- FREEMAN, J.S., CODY, F.W.J., CRAUFURD, D., NEARY, D. & SNOWDEN, J.S. (1993). Deficits of human rhythmic voluntary movements in Huntington's disease. *Journal of Physiology* **473**, 12P. [1]
- FREUND, H.J. (1986). Time control of hand movements. *Progress in Brain Research* **64**, 287-294. [4]
- GALVANI, L. (1791). *De Viribus Electricitatis*, translated by GREEN, R (1953) Cambridge, MA. [1]
- GARRETT, M., IRELAND, A. & LUCKWILL, R.G. (1984). Changes in the excitability of the Hoffmann reflex during walking in man. *Journal of Physiology* **355**, 23P. [1]
- GANONG, W.F. (1991). *Review of Medical Physiology*, 15th edition. Prentice-Hall International, London. [1]
- GASSER, H.S. & ERLANGER, J. (1922). The nature of conduction of an impulse in the relatively refractory period. *American Journal of Physiology* **73**, 613P. [1]
- GHEZ, C., GORDON, J., GHILARDI, M.F., CHRISTCOS, C.N. & COOPER, S.E. (1990). Roles of proprioceptive input in the programming of arm trajectories. *Cold Spring Harbor Symposia on Quantitative Biology* **55**, 837-847. [1]
- GOWERS, W.R. (1888). *A Manual of Diseases of the Nervous System*. Volume 2, pp. 656-674. Churchill, London. [6]
- GRILLNER, S. (1972). The role of muscle stiffness in meeting the changing postural and locomotor requirements for force development by ankle extensors. *Acta Physiologica Scandinavica* **86**, 92-108. [1]
- GRILLNER, S. (1975). Locomotion in vertebrates: central mechanisms and reflex interaction. *Physiological Reviews* **55**, 247-304. [1, 3]
- GRILLNER, S. (1979). Interaction between central and peripheral mechanisms in the control of locomotion. In *Reflex Control of Posture and Movement: proceedings of an IBRO symposium held in Pisa, Italy, on September 11-14, 1978*, ed. GRANIT, R. & POMPEIANO, O., pp. 227-235. Elsevier/North-Holland Biomedical Press, Amsterdam. [1, 3]
- GRILLNER, S. (1981). Control of locomotion in bipeds, tetrapods and fish. In *The Nervous System: Motor Control*, ed. BROOKS, V.B., Sect. 1, vol. 2 of Handbook of Physiology, pp. 1179-1236. American Physiological Society, Bethesda, MD [1]
- GRILLNER, S. (1985). Neurobiological bases of rhythmic motor acts in vertebrates. *Science* **228**, 143-149. [1]

- GRILLNER, S., DELIAGINA, T., EKEBERG, O., EL MANIRA, A., HILL, R.H., LANSNER, A., ORLOVSKY, G.N. & WALLEN, P. (1995). Neural networks that co-ordinate locomotion and body orientation in lamprey. *Trends in Neurosciences* **18**, 270-279. [3]
- GUIARD, Y. (1987). Asymmetric division of labour in human skilled bimanual action: The kinematic chain as a model. *Journal of Motor Behaviour* **19**, 486-517. [7]
- HAGBARTH, K.E. (1952). Excitatory and inhibitory skin areas for flexor and extensor motoneurones. *Acta Physiologica Scandinavica* Suppl. **26**, 1-58. [1]
- HAMMOND, P.H. (1954). Involuntary activity in biceps following the sudden application of velocity to the abducted forearm. *Journal of Physiology* **127**, 23-25. [5]
- HAMUY, T.P. (1956). Retention and performance of "skilled movements" after cortical ablations in monkeys. *Bulletin of the Johns Hopkins Hospital* **98**, 417-444. [1]
- HOFFMANN, P. (1918). Über die Beziehungen der Sehnenreflexe zur willkürlichen Bewegung und zum Tonus. *Zeitschrift für Biologie* **68**, 351-370. [1]
- HOFFMANN, P. (1922). *Untersuchung über die Eigenreflexe (Sehnenreflexe) menschlicher Muskeln*. Springer, Berlin. [1]
- HOLMES, G. (1917). The symptoms of acute cerebellar injuries due to gunshot injuries. *Brain* **40**, 461-535. [3]
- HOLMES, G. (1939). The cerebellum of man. The Hughlings Jackson memorial lecture. *Brain* **62**, 1-30. [7]
- HOUK, J.C. (1979). Regulation of stiffness by skeletomotor reflexes. *Annual Review of Physiology* **41**, 99-114. [1]
- HUMPHREY, D.R. & FREUND, H.J. (1991). Introduction. In *Motor Control: Concepts and Issues*, ed. HUMPHREY, D.R. & FREUND, H.J., pp. 1-4. John Wiley & Sons Ltd., New York. [1]
- HUGHES, M. & MCLELLAN, D.L. (1985). Increased co-activation of the upper limb muscles in writer's cramp. *Journal of Neurology, Neurosurgery and Psychiatry* **48**, 782-787. [1, 6]
- IBBOTSON, N.R. & MORTON, J. (1981). Rhythm and dominance. *Cognition* **9**, 125-138. [7]
- JAFFE, L. (1987). Influences of grip on legibility, speed, and fatigue in adult handwriting. Ph.D dissertation, Boston University. [4]
- JEANNEROD, M. (1994). Object oriented action. In *Insights into the Reach to Grasp Movement*, ed. BENNETT, K.M.B. & CASTIELLO, U., pp. 3-14. North-Holland, Amsterdam. [3]
- JENNER, J.R. & STEPHENS, J.A. (1982). Cutaneous reflex responses and their central nervous pathways studied in man. *Journal of Physiology* **333**, 405-419. [1, 5]
- JOHNSON, M.T.V., KIPNIS, A.N., LEE, M.C., LOEWENSON, R.B. & EBNER, T.J. (1991). Modulation of the stretch reflex during volitional sinusoidal tracking in Parkinson's Disease. *Brain* **114**, 443-460. [5]
- JONES, L. (1996). Proprioception and its contribution to manual dexterity. In *Hand and Brain*, ed. WING, A.M., HAGGARD, P. & FLANAGAN, J.R., pp. 349-362. Academic Press, London. [1]

- JONSSON, B. & KOMI, P.V. (1973). Reproducibility problems when using wire electrodes in electromyographic kinesiology. In *New Developments in Electromyography and Clinical Neurophysiology*. ed. DESMEDT, J.E., pp. 540-546. Karger, Basel. [2]
- KANDA, K. & SATO, H. (1983). Reflex responses of human thigh muscles to non-noxious sural stimulation during stepping. *Brain Research* **288**, 378-380. [1]
- KAPANDJI, I.A. (1987). *The Physiology of the Joints*, 5th edn. Churchill Livingstones, Edinburgh. [1]
- KELSO, J.A.S. (1982). The process approach to understanding human motor behaviour: An introduction. In *Human Motor Behaviour* ed. KELSO, J.A.S., pp. 3-19. Lawrence Erlbaum Associates, London. [1]
- KEOGH, J. & SUGDEN, D. (1985). *Movement Skill Development*. Macmillan, New York. [4]
- LANDSMEER, J.M.F. (1963). The co-ordination of finger-joint motions. *Journal of Bone and Joint Surgery* **45A**, 1654-1662. [1]
- LAWRENCE, D.G. & KUYPERS, H.G.J.M. (1968). The functional organisation of the motor system in the monkey: I. The effects of bilateral pyramidal lesions. *Brain*, **91**, 1-14. [1]
- LAWRENCE, J.H. & DE LUCA, C.J. (1983). Myoelectric signal versus force relationship in different human muscles. *Journal of Applied Physiology, Respiratory, Environmental and Exercise Physiology*. **54**, 1653-1659. [1, 3]
- LEE, R.G. & TATTON, W.G. (1975). Motor responses to sudden limb displacements in primates with specific CNS lesions and in human patients with motor system disorders. *Canadian Journal of Neurological Science* **2**, 285-293. [5]
- LEE, R.G. & TATTON, W.G. (1982). Long latency reflexes to imposed displacements of the human wrist: Dependence on duration of movement. *Experimental Brain Research* **45**, 207-216. [5]
- LEMON, R.N. (1981). Functional properties of monkey motor cortex neurones receiving afferent input from the hand and fingers. *Journal of Physiology* **311**, 497-519. [7]
- LEMON, R.N. (1983). Cortical control of the primate hand. *Experimental Physiology* **78**, 263-301. [1]
- LENNARD, P.R. & HERMANSON, J.W. (1985). Central reflex modulation during locomotion. *Trends in Neurosciences* **8**, 483-486. [1]
- LIDDELL, E.G.T. & SHERRINGTON, C.S. (1924). Reflexes in response to stretch (myotatic reflexes). *Proceedings of the Royal Society* **B96**, 212-242. [1]
- LIPPOLD, O.C.J. (1952). The relation between integrated action potentials in a human muscle and its isometric tension. *Journal of Physiology* **117**, 492-499. [2]
- LONG, C. & BROWN, M.E. (1964). Electromyographic kinesiology of the hand: muscles moving the long finger. *Journal of Bone and Joint Surgery* **46A**, 1683-1760. [1, 3]
- LONG, C., CONRAD, P.W., HALL, E.A. & FURLER, S.L. (1970). Intrinsic-extrinsic muscle control of the hand in power grip and precision handling. *Journal of Bone and Joint Surgery* **52A**, 853-867. [1]
- LUNDBERG, A. (1969). *Reflex Control of Stepping*. Universitetsforlaget, Oslo. [1]

- MAARSE, F.J. (1987). The study of handwriting movement: Peripheral models and signal processing techniques. PhD Thesis, Swets and Zeitlinger, Lisse. [7]
- MACKAY, W.A. & MURPHY, J.T. (1979). Cerebellar modulation of reflex gain. *Progress in Neurobiology* **13**, 361-417. [7]
- MAIER, M.A. & HEPP-REYMOND, M.C. (1995). EMG activity patterns during force production in precision grip. I. Contribution of 15 finger muscles to isometric force. *Experimental Brain Research* **103**, 108-122. [4]
- MAREY, E.J. (1873). *La Machine Animale. Locomotion Terrestre et Aerienne*. Bailliere, Paris. [1]
- MAREY, E.J. (1894). *Le Mouvement*. Masson, Paris. [1]
- MARSDEN, C.D., MERTON, P.A. & MORTON, H.B. (1972). Servo action in human voluntary movement. *Nature* **238**, 140-143. [5]
- MARSDEN, C.D., MERTON, P.A. & MORTON, H.B. (1976). Servo action in the human thumb. *Journal of Physiology* **257**, 1-44. [1, 5]
- MARSDEN, C.D., ROTHWELL, J.C. & DAY, B.L. (1984). The use of peripheral feedback in the control of movement. *Trends in Neurosciences* **7**, 253-257. [1]
- MARSDEN, C.D. & SHEEHY, M.P. (1990). Writer's cramp. *Trends in Neurosciences* **13**, 148-154. [1, 6]
- MATTEUCCI, C. (1844). *Traites des Phenomenen Electrophysiologiques*. Paris. [1]
- MATTHEWS, P.B.C. (1970). The origin and functional significance of the stretch reflex. In *Excitatory Synaptic Mechanisms*, ed. ANDERSEN, P. & JANSEN, J.K.S., pp 301-315. Universitetsforlaget, Oslo. [1, 5]
- MATTHEWS, P.B.C. (1984). Evidence from the use of vibration that the human long-latency stretch reflex depends upon spindle secondary afferents. *Journal of Physiology* **348**, 383-415. [5]
- MATTHEWS, P.B.C. (1986). Observations on the automatic compensation of reflex gain on varying the pre-existing level of motor discharge in man. *Journal of Physiology* **374**, 73-90. [1, 5]
- MATTHEWS, P.B.C. (1988). Proprioceptors and their contribution to somatosensory mapping: Complex messages require complex processing. *Canadian Journal of Physiology and Pharmacology* **66**, 430-438. [1]
- MATTHEWS, P.B.C. (1989). Long-latency stretch reflexes of two intrinsic muscles of the human hand analysed by cooling the arm. *Journal of Physiology* **419**, 519-538. [1, 5]
- MATTHEWS, P.B.C. (1991). The human stretch reflex and the motor cortex. *Trends in Neurosciences* **14**, 87-91. [1]
- MATTHEWS, P.B.C. (1993). Interaction between short- and long-latency components of the human stretch reflex during sinusoidal stretching. *Journal of Physiology* **462**, 503-527. [1, 5]
- MATTHEWS, P.B.C. (1994). The simple frequency response of human stretch reflexes in which either short- or long-latency components predominate. *Journal of Physiology* **481**, 777-798. [5]

- MATTHEWS, P.B.C., FARMER, S.F. & INGRAM, D.A. (1990). On the localisation of the stretch reflex of intrinsic hand muscles in a patient with mirror movements. *Journal of Physiology* **428**, 561-577. [1]
- MCGEER, P.L. & MCGEER, E.G. (1980). The control of movement by the brain. *Trends in Neurosciences* **3**, 3-4. [1]
- MERTON, P.A. (1953). Speculations on the servo-control of movements. In *The Spinal Cord*, ed. WOLSTENHOLME, G.E.W., pp. 247-255. CIBA Foundation Symposium Churchill, London. [1]
- MEULENBROEK, R.G.L. (1989). A study of handwriting production: Educational and developmental aspects. PhD Thesis, University of Nijmegen, Netherlands. [7]
- MILANOV, I. (1992). A comparative study of methods for estimation of presynaptic inhibition. *Journal of Neurology* **239**, 287-292. [6]
- NAKASHIMA, K., ROTHWELL, J.C., DAY, B.L., THOMPSON, P.D. & MARSDEN, C.D. (1990). Cutaneous effects on presynaptic inhibition of flexor Ia afferents in the human forearm. *Journal of Physiology* **426**, 369-380. [1]
- NAKASHIMA, K., ROTHWELL, J.C., DAY, B.L., THOMPSON, P.D., SHANNON, K. & MARSDEN, C.D. (1989). Reciprocal inhibition between forearm muscles in patients with writer's cramp and other occupational cramps, symptomatic hemidystonia and hemiparesis due to stroke. *Brain* **112**, 681-697. [6]
- NAPIER, J.R. (1956). The prehensile movements of the human hand. *Journal of Bone and Joint Surgery* **38B**, 902-913. [1]
- NOTH, J., PODOLL, K. & FRIEDEMANN, H.H. (1985). Long loop reflexes in small hand muscles studied in normal subjects and in patients with Huntington's disease. *Brain* **108**, 65-80. [1]
- NOTH, J. & SCHWARZ, M. (1991). Difference in reflex control of distal and proximal arm muscles as revealed in patients with central motor disorders. In *Muscle Afferents and Spinal Control of Movement*, ed. JAMI, L., PIERROT-DESEILLIGNY, E. & ZYTNIICKI, D., pp. 421-426. IBRO Symposium, Pergamon Press, Oxford. [5]
- NOTH, J., SCHWARZ, M., PODOLL, K. & MOTAMEDI, F. (1991). Evidence that low-threshold muscle afferents evoke long-latency stretch reflexes in human hand muscles. *Journal of Neurophysiology* **65**, 1089-1097. [1, 5]
- O'BOYLE, D.J., FREEMAN, J.S. & CODY, F.W.J. (1996). The accuracy and precision of timing of self-paced, repetitive movements in subjects with Parkinson's disease. *Brain* **119**, 51-70. [1]
- OGUZTORELI, M.N. & STEIN, R.B. (1976). The effects of multiple reflex pathways on the oscillations in neuromuscular systems. *Journal of Mathematical Biology* **3**, 87-101. [7]
- OPPENHEIM, H. (1911). *Neurologisches Zentralblatt* **30**, 1090-1107. [6]
- PAULIGNAN, Y., DUFOSSE, M., HUGON, M. & MASSION, J. (1989). Acquisition of co-ordination between posture and movement in a bimanual task. *Experimental Brain Research* **77**, 337-348. [3]
- PENFIELD, W. & RASMUSSEN, T. (1950). *The Cerebral Cortex of Man*. Macmillan, New York. [1]

- PETERS, M. (1981). Attentional asymmetries during concurrent bimanual performance. *Quarterly Journal of Experimental Psychology* **33A**, 95-103. [7]
- PHILLIPS, C.G. (1969). Motor apparatus of the baboon's hand. *Proceedings of the Royal Society* **173**, 141-174. [5, 7]
- PHILLIPS, C.G. (1986). *Movements of the Hand*. Liverpool University Press, Liverpool. [1]
- PIPER, H. (1907). Über den willkürlichen Muskeltetanus. *Pflügers Archiv Ges Physiol Mensch Tiere* **119**, 301-339. [1]
- PIPER, H. (1912). Die Aktionsströme menschlicher Muskeln. Die Methodik der Untersuchung am Seitengalvanometer und die Prinzipien der Stromkurvenanalyse. Typenunterschiede der Willkürkontraktion. *Z. biol. tech. Methode* **3**, 52. [1]
- POORE, G.V. (1878). An analysis of 75 cases of writer's cramp and impaired writing power. *Transactions of the Royal Medical and Chirurgical Society* **61**, 111-145. [6]
- POORE, G.V. (1897). *Nervous Affections of the Hand and Other Clinical Studies*. pp. 26-75. Elder, Smith, London. [6]
- PROEBSTER, R. (1928). Über Muskelaktionsströme am gesunden und kranken Menschen. *Orthopaedic Clininic* **50**, 1. [1]
- REIS, G.V. (1954). Electromyographical studies in writer's cramp. *Acta Medica Scandinavica* **149**, 253-260. [6]
- RISPAL-PADEL, L., CICIRATA, F. & PONS, J.C. (1982). Cerebellar nuclear topography of simple and synergistic movements in the alert baboon. *Experimental Brain Research, Supplement* **47**, 365-380. [7]
- RISPAL-PADEL, L., CICIRATA, F. & PONS, J.C. (1983). Neocerebellar synergies. *Experimental Brain Research* **7**, 213-223. [7]
- ROSENBLOOM, L. & HORTON, M.E. (1971). The maturation of fine prehension in young children. *Developmental Medicine and Child Neurology*, **13**, 3-8. [4]
- ROTHWELL, J.C. (1994). *Control of Human Voluntary Movements*, 2nd edn. Chapman & Hall, London. [7]
- ROTHWELL, J.C., OBESO, J.A., DAY, B.L. & MARSDEN, C.D. (1983). Pathophysiology of dystonias. *Advances in Neurology* **39**, 851-863. [1, 6]
- ROTHWELL, J.C., TRAUB, M.M., DAY, B.L., OBESO, J.A., THOMAS, P.K. & MARSDEN, C.D. (1982). Manual motor performance in a deafferented man. *Brain* **105**, 515-542. [1]
- SAIDA, Y. & MYASHITA, M. (1979). Development of fine motor skill in children: manipulation of a pencil in young children aged 2-6 years old. *Journal of Human Movement Studies* **5**, 104-113. [4]
- SASSOON, R.S. (1988). Joints in children's handwriting: The effects of different models and teaching methods. PhD Thesis, University of Reading. UK. [7]
- SCHIEBER, M.H. (1996). Individual finger movements. In *Hand and Brain*. ed. WING, A.M., HAGGARD, P. & FLANAGAN, J.R., pp. 81-98. Academic Press, London. [1]
- SCHIEPPATI, M. (1987). The Hoffmann reflex: a means of assessing spinal reflex excitability and its descending control in man. *Progress in Neurobiology* **28**, 345-376. [1]

- SCHMIDT, R.A., ZELAZNIK, H.N., HAWKINS, B., FRANK, J.S. & QUINN, J.T. (1979). Motor-output variability: A theory for the accuracy of rapid motor acts. *Psychological Review* **86**, 415-451. [7]
- SCHMOKER, L.R.B. (1991). Simulation and recognition of handwriting movements: A vertical approach to modelling human motor behaviour. PhD Thesis, University of Nijmegen. [7]
- SCHNECK, C.M. (1991). Comparison of pencil-grip patterns in first graders with good and poor writing skills. *The American Journal of Occupational Therapy* **45**, 701-706. [1]
- SCHNECK, C.M. & HENDERSON, A. (1990). Descriptive analysis of the developmental progression of grip position for pencil and crayon control in non-dysfunctional children. *The American Journal of Occupational Therapy* **44**, 893-900. [1, 4]
- SERGIO, L.E. & OSTRY, D.J. (1994). Co-ordination of mono- and bi-articular muscles in multi-degree of freedom elbow movements. *Experimental Brain Research* **97**, 551-555. [3]
- SHEEHY, M.P. & MARSDEN, C.D. (1982) Writers' cramp. A focal dystonia. *Brain* **105**, 461-480. [4, 6]
- SHEEHY, M.P., ROTHWELL, J.C. & MARSDEN, C.D. (1988). Writer's cramp. *Advances in Neurology* **50**, 457-472. [1, 4, 6]
- SHERINGTON, C.S. (1906). *The Integrative Action of the Nervous System*. Yale University Press, New Haven, CT. [1]
- SHERINGTON, C.S. (1910). Flexion of the limb crossed extension reflex, and reflex stepping and standing. *Journal of Physiology* **40**, 28-121. [1]
- SHERINGTON, C.S. (1915). Posture activity of muscle and nerve. *Brain* **38**, 191-234. [1]
- SMITH, P (1977). *Developing Handwriting*. Macmillan Education Ltd., London. [1]
- SOECHTING, J.E. & LACQUANITI, F. (1981). Invariant characteristics of a pointing movement in man. *Journal of Neuroscience* **1**, 710-720. [7]
- SOLLY, S. (1864). Clinical lectures on scriveners' palsy or the paralysis of writers. *Lancet* **2**, 709-711. [6]
- SPENCER, A.P. & MASON, E.B. (1992). *Human Anatomy and Physiology*. West Publishing Company, New York. [2]
- STEIN, R.B. (1995). Presynaptic inhibition in humans. *Progress in Neurobiology* **47**, 533-544. [1, 3, 5, 6]
- STEIN, R.B. & CAPADAY, C. (1988). The modulation of human reflexes during functional motor tasks. *Trends in Neurosciences* **11**, 328-332. [1, 5, 6, 7]
- STONE, R.J. & STONE, J.A. (1990). *Atlas of the Skeletal Muscles*. Wm. C. Brown, Dubuque, Iowa. [2]
- STRICK, P.L. & PRESTON, J.B. (1982). Two representations of the hand in area 4 of a primate. II Somatosensory input organisation. *Journal of Neurophysiology* **48**, 150-159. [7]
- TEASDALE, N., FORGET, R., BARD, C., PAILLARD, J., FLEURY, M. & LAMARRE, Y. (1993). The role of proprioceptive information for the production of isometric forces and for handwriting tasks. *Acta Psychologica* **82**, 179-191. [1]

- TEULINGS, H.L. (1996). Handwriting movement control. In *Motor Skills*, vol. II, *Handbook of Perception and Action*, ed. HEUER, H. & KEELE, S.W., pp. 561-613. Academic Press, London. [7]
- THACH, W.T., GOODKIN, H.P. & KEATING, J.G. (1992). The cerebellar and the adaptive co-ordination of movement. *Annual Review of Neuroscience* **15**, 403-42. [7]
- THACH, W.T., SCHIEBER, M.H., MINK, J.W., KANE, S.A. & HORNE, M.K. (1986). Cerebellar relation to muscle spindles in hand tracking. *Progress in Brain Research* **64**, 217-224. [7]
- THILMANN, A.F., SCHWARZ, M., TÖPPER, R., FELLOWS, S.J. & NOTH, J. (1991). Different mechanisms underlie the long-latency stretch reflex response of active human muscle at different joints. *Journal of Physiology* **444**, 631-643. [1]
- TORTORA, G.J. & ANAGNOSTAKOS, N.P. (1990). *Principles of Anatomy and Physiology*. 6th edn. Harper Collins, New York. [1]
- TRAVIS, A.M. (1955). Neurological deficiencies after ablation of the precentral motor area in *Macaca mulatta*. *Brain* **78**, 155-173. [1]
- VERCHER, J.L. & GAUTHIER, G.M. (1988). Cerebellar involvement in the co-ordination control of the oculo-manual tracking system: Effects of cerebellar dentate nucleus lesion. *Experimental Brain Research* **73**, 155-166. [3]
- WEISER, D. (1986). Handwriting: Assessment and remediation. *Developmental Disabilities Special Interest Section Newsletter*, 1-3. [4]
- WESTPHAL, C. (1875). Über einige Bewegungs-Erscheinungen an gelähmten Gliedern. *Archiv für Psychiatrie* **5**, 803-834. [1]
- WILLIAMS, P.L., WARWICK, R., DYSON, M. & BANNISTER, L.H. (1989). The nature of dexterity. In *Gray's anatomy*, 37th edn. pp. 632-635. Churchill Livingstones, Edinburgh. [3, 7]
- WOOLSEY, C.N., SETTLAGE, P.H., MEYER, D.R., SENCER, W., HAMUY, T.P. & TRAVIS, A.M. (1951). Patterns of localisation in precentral and "supplementary" motor areas and their relation to the concept of a premotor area. *Research Publications of the Association for Research in Nervous and Mental Disorders*, **30**, 238-264. [1]
- WYNN-PARRY, C.B. (1966). *Rehabilitation of the Hand*, 2nd edn. Butterworth, London. [3, 4]
- WYNN-PARRY, C.B. (1981). *Rehabilitation of the Hand*, 4th edn. Butterworth, London. [3]
- XIA, R. & BUSH, B.M.H. (1995). Co-ordination of human hand muscles during rhythmic finger movements related to writing. *Journal of Physiology* **483.P**, 133P. [2, 3]
- XIA, R. & BUSH, B.M.H. (1996a). Hand muscle EMG patterns during repetitive 'writing' tasks in people with different pen grips. *Journal of Physiology* **491.P**, 84-85P. [2, 4]
- XIA, R. & BUSH, B.M.H. (1996b). EMG phase analysis of rhythmic manipulations and phase-dependent reflexes in human hand muscles. *Journal of Physiology* **493.P**, 8-9P [1, 2]
- XIA, R. & BUSH, B.M.H. (1996c). Phase-dependent modulation of reflex gain during repetitive finger actions in man. *Journal of Physiology* **497.P**, 108P [2, 5]

- XIA, R. & BUSH, B.M.H. (1996d). Phase-dependent modulation of reflex responses during repetitive manipulative tasks related to handwriting. *Proceedings of the 11th congress of the International Society of Electrophysiology and Kinesiology* pp. 174-175. [2, 5]
- YANG, J.F. & STEIN, R.B. (1990). Phase-dependent reflex reversal in human leg muscles during walking. *Journal of Neurophysiology* **63**, 1109-1117. [2, 5]
- ZIVIANNI, J. & ELKINS, J. (1986). Effect of pencil grip on handwriting speed and legibility. *Educational Review* **38**, 247-257. [4]